Intensive Segregation, or Divergence through Independent Transformation. By Rev. JOHN THOMAS GULICK. (Communicated by W. PERCY SLADEN, F.L.S.)

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IN a previous paper on "Divergent Evolution through Cumulative Segregation"* I have enumerated eighteen classes of natural causes which produce either Separate or Segregate Generation †, and which, in their combined action, tend to produce cumulative Segregation and divergent evolution in every part of the organic world. I have there shown, with sufficient fulness, that cumulative Segregation always produces cumulative divergence or polytypic evolution; but I have not fully shown how Separation from the first involves more or less Segregation, or how Segregation, that at first divides the species into sections with reference to some one endowment, is always tending toward intensified Segregation in which the sections present differences in regard to an increasing number of endowments.

After expounding the principles on which these laws of divergence rest, I will give a few examples of divergence, calling attention to the complete correspondence between the facts of nature and the principles expounded in this and the previous paper.

Separation always involves more or less Segregation, for no two portions of a species possess exactly the same average character. When a homogeneous species is divided into two large sections,

* Journ. Linn. Soc., Zool. vol. xx. pp. 189–274.

† Separate Generation, or Separation, is the indiscriminate division of a species into sections that do not intergenerate. Segregate Generation, or Segregation, is the Independent Generation of different sections of a species when the sections are composed of somewhat divergent classes of variations. Segregation differs from Selection in that the latter denotes the exclusion of certain kinds from opportunity to propagate, while the former denotes the division of those that propagate into classes that are prevented from intergenerating. I use intergenerate rather than interbreed that I may have a term equally applicable to plants and to animals. Independent Generation, or the prevention of intergeneration, whether it be through Separation or Segregation, I sometimes call Segeneration. Darwin used Isolation as equivalent to geographical separation, while later writers have sometimes used it as equivalent to Independent Generation. Following Darwin, I use it for distribution in different areas, especially when barriers intervene.

it may be difficult to prove by measurement that there is any difference in their average character; but on general principles we may assume that, at least in some points, there is a slight difference. It is evident that when the separated sections are small there is more likely to be *diversity* in the average character of the sections, and that, roughly stated, the probability of divergence from this cause will be in direct proportion to the variableness of the species, and in inverse proportion to the size of the different sections. When a few stragglers form a small colony in an isolated position there is the strongest reason to expect that they will not be able to propagate the characters of the species in exactly the same proportions in which they are produced by the main body of the species, or by any other small colony that is propagating independently; and when the original stock has been rendered highly variable by the crossing of somewhat divergent varieties, the degree of difference that will probably be presented by any two independent colonies will be correspondingly increased. We must bear in mind that, while specimens possessing an average character in any one respect are always abundant, those perfectly representing the average in every respect are rarely, if ever, found. Now, is it to be supposed that any one, or any small number of these imperfect representatives of a species will, if separated from the rest, transmit all the characteristics of that species in the exact proportions presented by the average character of the original stock?

Mr. Francis Galton has conclusively shown* that in the children of parents whose heights deviate from the average of the race to which they belong there will be a similar deviation amounting on the average to a certain fixed proportion of that presented by what he calls the mid parentage. The mid-filial deviation in the groups investigated by him was about two thirds of the mid-parental deviation. There is therefore a regression in the average character of the offspring toward the typical character of the group. It must be observed, however, that this law can hold in full force only where there is free crossing, otherwise no divergent race could ever be formed by any amount of selection and independent breeding.

* See "Types and their Inheritance," an address before the Section of Anthropology of the British Association in 1885; also 'Natural Inheritance,' p. 97.

Eight Principles of Monotypic Evolution.

Let us now consider how this initial Segregation, which is always present where migration or geological subsidence produces indiscriminate Separation, is enhanced and intensified by the cooperation of other principles, and how forms, segregated through possessing different characters in some one respect, come to diverge in other respects. For example, when differences of colour become the occasion for sexual and social Segregation, how does this open the way for divergent transformation in habits of feeding and in a thousand other respects? The principles co-operating with Independent Generation in producing this enhanced divergence are all causes of simple transformation, or monotypic evolution when there is free intergeneration. Divergent breeds of domestic animals have always been produced when the different sections of a species in the care of different races of men have been prevented from interbreeding, thus securing their Independent Transformation during the process of domestication. So in nature, when any form of Independent Generation has been established, any cause of transformation that may afterwards arise will always produce more or less divergent evolution, and never that which is in every respect parallel. But we must defer the discussion of this subject till we have enumerated the more manifest of the principles of monotypic evolution:—

1. *Assimilational Transformation*, or modification due to deficiency with economy, or redundance with profusion, of growth, resulting from different degrees of assimilative power. "Economy of growth" is a term already in use, but a term is needed that shall include both this and its opposite.

2. *Stimulational Transformation*, or modification produced by changed motions in the fluids of an organism responsive to changed molecular influences in the environment. Under this principle we may place the direct influences of light, heat, electricity, the dampness of the air or the saltness of the water in which the organism is bathed, the quality of the food, and all stimulation from physical and chemical causes, exclusive of those resulting in muscular activity or the movement of organs.

3. *Suetudinal Transformation*, or modification due to the effects of use, disuse, and habitual effort in producing motions, and in resisting the strain of gravity and other forces tending to produce motion. Suetude is not found in the dictionary, but I venture

to use it as including both assuetude, which is being accustomed to, being practised in, habitual use,—and desuetude, which is disuse, discontinuance of practice. This principle has been recognized by most biologists, though it has recently been called in question by Weismann.

4. *Emotional Transformation.*—Dr. C. V. Riley, of the National Museum, Washington, has called attention to the influence of parental emotions, especially maternal emotions during the term of pregnancy, as a factor in evolution (Address " On the Causes of Variation," before the Section of Biology, American Association, August 1888; also in 'Popular Science Monthly,' vol. xxxiv. pp. 811–816).

5. The cumulative development of adaptations through " the survival of the fittest " when the fittest are other than average forms. This is the principle of *Unbalanced Selection* or of *Selectional Transformation.*

6. Transformation produced by the indiscriminate destruction of a portion of a species, with the accompanying probability that the remaining portion will not possess all the characters possessed by the species previous to the elimination. This principle I call *Unbalanced Elimination*, or *Eliminational Transformation.*

7. Transformation produced by different degrees of amalgamation of the varieties and races which have resulted from previous Segregations. In most species there is a constant process of amalgamation by which thousands of minor varieties are absorbed; but when the process proceeds beyond ordinary limits, and the barriers that have divided well-marked races give way, transformation must follow. This principle I call *Diversity of Amalgamation*, or *Amalgamational Transformation.*

8. The cumulative development of the more fertile of the forms that are equally adapted. In other words, transformation produced by diversity in the relative fertility of varieties that are equally adapted to the environment and the constitution of the species, or by change in the degrees of fertility possessed by the same variety at different times and in different places. This principle I call *Unbalanced Fecundity*, or *Fecundal Transformation.*

Of these principles, all, except the 6th, 7th, and 8th, have been more or less discussed by writers on biology, though some of the forms of Selection depending on the relations in which the members of a species stand to each other have never been pointed out, and many writers have failed to observe that natural selection often produces fixity of type instead of transformation, and that divergence in the kinds of natural selection depends on Segregation, and not necessarily on exposure to different environments.

Assimilational, Stimulational, Suetudinal, and Emotional Transformation belong to a class of principles that have sometimes been grouped under the term Variation, while Selectional, Eliminational, Amalgamational, and Fecundal Transformation may be classed as *principles of Unbalanced Propagation*. It should, however, be carefully noted that Variation usually indicates deviation from the average, an entirely different factor from those which relate to the change of the average itself. It may therefore be well to group these first four principles as *principles of Involution*. The principles of Unbalanced Propagation are abundantly established as genuine methods of change in the average inheritable characters of species, not only by experience derived from the domestication of plants and animals, but by observation of similar effects produced by natural processes. On the other hand, the principles of Involution, though very marked in their influence on individual character, cannot be easily tested as to their effects on the inheritable characters of species. Weismann maintains that acquired characters cannot be inherited. If this is so, there can be no involution of specific characters, and the only factors in monotypic evolution are the causes whose laws of action are expressed in the principles of Unbalanced Propagation.

I have not mentioned "Acceleration and Retardation" as principles of transformation, for they seem to be but phases of the law of Suetude; for, as explained by Cope, the former is the effect of Use or Effort in the parents, producing in the offspring accelerated inheritance, while the latter is due to Disuse or Cessation from Effort, producing in the offspring retarded inheritance *. So also Hyatt's "law of Concentration" (or "Acceleration," as he often calls it) seems to be a general law of inheritance relating to the transmission of characters originating under any and every principle, the effects, whether progressive or retrogressive, being inherited at earlier and earlier ages in each successive generation †. It is also doubtful whether Correlated

* 'Origin of the Fittest,' pp. 203–7, 228.

† 'Proceedings of the American Association,' vol. xxxii. pp. 352–361.

Transformation should be considered a separate principle, for it seems to be simply the inheritance by offspring of characters that have for many generations been united in the endowments of at least a portion of their ancestry, and the correlation of these endowments must have been produced through the action of other principles.

The prevalence of males in times of pressure, with the prevalence of females in times of plenty, is regarded by Dr. W. K. Brooks, of Johns Hopkins University, as a characteristic established by natural selection, by which the organism acquires variability or fixity of type according as either character is most needed; for according to his observations the males represent the former, and the females the latter element. There can be no doubt that in many species the males are more variable than the females, and that in some of the same species the proportion of males increases with the degree of adversity; but this does not seem to be sufficient ground for maintaining that the increase in the proportion of males will increase the variability of the offspring. Increase in the number or amount of the variable element does not necessarily involve increase in the variability of either element, or in the offspring of both. I find need of additional factors in order to bring these facts into any relation to the increase of variability. Granting that the sperm-cell is the source of variation and the germ-cell the source of fixity, and that increased tendency to variation in the offspring will be secured by an increased range of variation in the sperm-cells, it does not follow that increase in the relative number of males will increase the range of variation in the sperm-cells, and therefore in the offspring. But if conflict with the environment and the winnowing process of natural selection falls most heavily upon the males, there must be some advantage in having their relative numbers increased in times of adversity; and if the exposure of parents to hardships increases the variability of either male or female offspring, and especially if it increases the variability of both, plasticity will be increased.

Prof. Cope's "Doctrine of the Unspecialized" ('Origin of the Fittest,' pp. 232–5) rests on the fact that the most highly specialized types, as well as individuals, are most likely to be exterminated by extraordinary changes in the environment; and Mr. Hyatt's "Geratology" ('Proceedings of the American Association,' vol. xxxii. pp. 349, 360) teaches that types that are being slowly exterminated usually assume forms resembling those produced by old age and disease in the individual. These and other parallel laws in the growth and decay of types and individuals are of great interest, as they afford organic conditions under which the principles of transformation must act.

After considering certain general propositions that apply equally to all of the eight principles above enumerated, I shall consider more particularly what the effect of some of these principles is when cooperating with Independent Generation. The only principles I shall treat in this special way are the four principles of Unbalanced Propagation.

The Transformation of freely Intergenerating Organisms never Divergent.

I mention these eight principles of transformation, not with the purpose of entering upon a full discussion of the same, but simply to point out the relation in which they all stand to divergent, or polytypic, evolution. It is evident that whether acting separately or together, they can never be the cause of divergent evolution in organisms that are freely intergenerating; for in such a group of organisms whatever modifies one part of the group in characters that are inheritable will ere many generations modify the whole. If the group is exposed to a variety of inharmonious conditions, which with Independent Generation would produce divergent character, with free Intergeneration the only result will be variation. Without Segregation there can be no permanent divergence; and with Segregation there must be divergence; and with cumulative Segregation there must be cumulative divergence. This principle, which I call *Divergence through Segregation*, was the subject of my previous paper.

Independent Transformation never Parallel, but always Divergent.

If any species is divided into two or more sections that do not intergenerate and that are severally subject to highly complex transforming influences, it can only be by a series of coincidences which the reason refuses to receive as in the slightest degree probable that any two sections will be modified in exactly the same way. This high degree of probability, amounting to a certainty, that when causes of transformation cooperate with causes producing Separation or Segregation, the result in successive generations will be increasing degrees of Segregation and of divergence, is what I call the law of *Intensive Segregation.* The different forms of this principle, resting on the certainty that the cooperation of any one of the principles of transformation with any one of the principles of independent generation will produce increasing Segregation with increasing divergence, are the following :—

1. *Assimilational Intension*, or Segregation and Divergence through Independent Assimilation.
2. *Stimulational Intension*, or Segregation and Divergence through Independent Stimulation.
3. *Suetudinal Intension*, or Segregation and Divergence through Independent Suetude.
4. *Emotional Intension*, or Segregation and Divergence through Independent Emotional Transformation.
5. *Selectional Intension*, or Segregation and Divergence through Independent Selection.
6. *Eliminational Intension*, or Segregation and Divergence through Independent and indiscriminate Elimination.
7. *Amalgamational Intension*, or Segregation and Divergence through Independent Amalgamation.
8. *Fecundal Intension*, or Segregation and Divergence through Independent Fecundal Transformation.

In groups that do not intergenerate, divergent forces reveal themselves whenever transformation is introduced. If it were possible to believe that in any case the effects of Independent Selection or of Independent Suetude had been completely parallel, it would still be impossible to believe that both of these, together with the remaining six principles of transformation, would ever so combine as to produce completely parallel effects. It is a familiar fact that no two persons are exactly alike ; and it is probably true that no two groups of any organism are exactly alike. Though we cannot fully explain the fact *we accept as a certainty the non-equivalence of biological quantities* ; and consequently we assume with confidence that there cannot be completely parallel transformation in isolated sections of a species, even if all are surrounded by the same environment. This principle is not inconsistent with the production of what Prof. Hyatt calls "representative or parallel characteristics" in two or more divergent series of forms. What he points out is that, under the influence of heredity, similar organisms exposed to similar environments undergo similar transformation ('Anniversary Memoirs of the Boston Society of Natural History,' 1880; "The Genesis of the Tertiary Species of *Planorbis* at Steinheim," pp. 24–29).

In the description of these principles I have used the adjective "Independent" to signify that the principle is operating in sections of the species that are prevented from intergenerating. If Isolated Selection were used instead of Independent Selection, it would be constantly liable to be understood as meaning Selection acting upon sections produced simply by geographical separation; for Darwin never used Isolation to designate the prevention of free crossing in other ways. In the term "Independent Variation" Mr. Romanes has already used the adjective "*Independent*" as meaning "*when accompanied with the prevention of intercrossing*;" and as it is less likely to be misunderstood, I prefer it. Part of what Romanes indicates by "Independent Variation" is, I think, in my scheme distributed between the four principles of Assimilational, Eliminational, Amalgamational, and Fecundal Transformation when acting on independent groups. As these principles are quite distinct, the separate names will be a convenience. If there are other forms of transformation, the causes of which cannot be given, I would prefer to class them as due to unknown causes rather than attribute them to Variation, which, as there used, is only a name for unexplained transformation. I would not turn Variation from its usual meaning, which is deviation from the average character of an intergenerating group.

The Pervasive Influence of the Causes of Transformation, and the Law of Intension.

In my paper on "Divergent Evolution through Cumulative Segregation," p. 215, I made the statement that, "When Separate Generation is long continued, we have reason to believe, it always passes into Segregate Generation with divergent evolution." The same had been expressed in a previous paper by the statement that "Variation is so strong, that all that is necessary to secure a divergence of types is to prevent their intermingling"*. The certainty that Independent Generation with transformation will never produce parallel, but always more or

* "Diversity of Evolution under one Set of External Conditions," Journ. Linn. Soc., Zool. vol. xi. p. 499.

less divergent evolution is *the law of Intensive Segregation* already referred to; but in addition to this certainty there is a very strong probability that where Independent Generation is long continued, transformation of some kind will supervene. If there are any species in which the power of cumulative variation has been entirely lost, this latter law cannot hold in their case; but it is doubtful whether among species that reproduce sexually there are many such. The variability of some species is so small, and the conditions of the environment are so constant, that comparatively long periods of Independent Generation pass before perceptible transformation arises. This seems to be the case with the 13- and 17-year races of *Cicada septemdecim*, to which I shall refer when giving examples from nature. From the high probability that long-continued Independent Generation will be followed by Independent Transformation, and the certainty that Independent Transformation will be divergent, there follows the corollary that long-continued Independent Generation will probably be attended by divergence. In other words, Independent Generation long continued is almost always attended by Independent Transformation; and Independent Transformation inevitably produces Divergence. This double principle I call *the law of Intension.* This law rests on the ubiquity of transforming influence, and on the impossibility that in a species possessing any plasticity the inherited effects in any section independently generating should be exactly the same as in any other section.

We cannot doubt that, when a diversity of powers and susceptibilities in the different sections is acted upon by a great variety of influences, the responses of the different sections will be unlike; and the result will be increasing segregation and increasing divergence. Now it is impossible to doubt that in species propagating sexually, and possessing some degree of plasticity, these are exactly the conditions whenever the species is divided into sections that do not intergenerate.

It should be observed that, in accordance with the principle of Intension, not only is indiscriminate Separate Generation when long continued transformed into more and more strongly Segregate Generation, but any form of Segregate Generation, resting on some one principle that causes the division of the species into sections differing in regard to some one form of endowment, will, if long continued, be inevitably reinforced and intensified by transformations, which, being independently combined and transmitted, will multiply the number of characteristics in regard to which divergence takes place. If, for example, the pollen of a given variety, when falling upon the stigma of the same variety or race, is impotent over the pollen of any other variety or race that falls upon the same stigma at the same time, or at a somewhat earlier time, what I call Prepotential Segregation will divide the species into two groups that are prevented, for the most part, from intergenerating; and these separate groups, gradually coming under the influence of different degrees, forms, and combinations of the transforming principles, will in time become strongly characterized species. It is not, however, necessary that all or any of these forms of transformation should cooperate with Segregation in order to produce a distinct species. The accumulated effects of Segregation, unaided by these principles of transformation, would be sufficient to produce well-defined species; but it is impossible that they should often remain unaided.

As the law of Intension is one of the most general of the laws relating to divergent evolution, it is not strange that the principles through which it is made evident are of a general nature. The marvel is that concerning so wide a law the evidence is so complete.

Utilitarian and Non-Utilitarian Divergence.

The principles of Suetude and Selection are directly related to the development of utilitarian characters; but the effects of the other six principles are often not only wanting in, but opposed to, utility. Assimilational Transformation includes redundance of growth, which is not always, as well as economy of growth, which is always, utilitarian. Some of the inherited effects of Stimulation and Emotion fortify the constitution against the destructive influences of the environment, while others leave the offspring more exposed than the parent. Unbalanced Elimination, Amalgamation, and Fecundity may be advantageous, useless, or disadvantageous. We have, therefore, in these six principles of transformation abundant cause for the introduction of non-utilitarian characters; and, when accompanied by Independent Generation, they must be the source of multitudes of non-utilitarian divergences. In the earlier stages of divergent evolution the non-utilitarian distinctions are more abundant; for in the later stages multitudes of them are weeded out by economy of growth (as has been clearly pointed out by Mr. Romanes *); and still others, through coming under new conditions in the environment or through some new habit of intelligence, become useful endowments, and are brought under the preserving and accumulating influence of Natural Selection or of Suetude. It should, however, be noted that the development of useful specific differences is as much due to Independent Generation as is the development of useless specific differences. Diversity of Suetude or of Selection does not produce divergent evolution unless it cooperates with Independent Generation.

Selectional Intension, or *Segregation and Divergence produced by Independent Selection.*

That we may gain a clear apprehension of the nature and influence of this principle, certain discriminations, which have not always been recognized by writers on the subject, are absolutely necessary; and, for the sake of avoiding misunderstandings, it is desirable that these distinctions should be represented by clearly defined terms. I am fully aware that many will be opposed to the introduction of new terms into the treatment of a subject that has been so long and so ably discussed. If these discriminations were not found necessary by the author of the 'Origin of Species,' or if the distinctions, so far as recognized by himself and others, have been expressed in the language of ordinary description, why should a more accurate terminology be needed now? In reply, it may be said that the freedom from technical language which is a great advantage in a work which for the first time calls attention of the world to a vast subject, is a serious defect when the exact relations of the subject come under discussion.

In order to secure clear thinking on the subject, I have found it necessary to keep the following distinctions constantly in mind:—

(1) The Selection that results in the transformation of species is not the selection of one species to the exclusion of another. The breeding of the horse to the exclusion of the ass modifies neither the one nor the other. It is the exclusive generation of certain variations of a single intergenerating group that gradually

* "Physiological Selection," Journ. Linn. Soc., Zool. vol. xix. p. 383.

transforms the group. When, therefore, we speak of Selection as a cause of transformation, we refer to the Selection of the variations that are to interbreed and keep up the race, to the exclusion of other variations. In order to maintain the same distinction in the nomenclature of natural processes, what I call *Selection* is caused by the failure of certain forms of a species to perpetuate their kind as contrasted with the success of other forms. If the failure includes all the forms of a species, I call it the *Extinction* of that species, and class it as a cause of transformation in the remaining species only so far as it makes a change in their environment.

(2) The exclusive generation of certain forms of an intergenerating group does not necessarily result in transformation. Experiments in artificial breeding show that if we select only the typical representatives of a race, the general character of the race is not changed, though any tendency to fluctuating variation may be gradually diminished, and the stability of the type increased. When, however, one form of deviation from the mean is constantly selected without a counterbalancing selection of the opposite deviation, the transformation of the race is always the result. In other words, *Balanced Selection produces Stability of Type, and Unbalanced Selection produces Transformation of Type.*

In the light of this twofold law we see how there may be stringent Natural Selection without transforming effect. It has sometimes been maintained that the transformation of species through the Natural Selection of favoured races is a necessary process which must be operating in nearly every species; for in nearly every species there is a constant struggle between the different forms of variation; and as it never happens that all the forms are equally successful, the process of Natural Selection is always bearing in full force upon the species. If it could be shown that Natural Selection, wherever it exists, must necessarily produce transformation, it would be impossible to resist the conclusion that nearly every species is undergoing transformation through this cause. But it is Unbalanced, and never Balanced, Selection that produces transformation. We also see that heredity tends to make the most successful form the average form, and thus to convert Unbalanced into Balanced Selection. From this it follows that in order that Selection should produce continuous transformation, it is necessary that the form of variation selected should from time to time be changed. This may be expressed as the law of *Continuous Transformation through Successive Changes in the Character of the Selection.*

Though Selection produces transformation only when it involves the survival of other than typical forms, it is still very possible that there are but few species in which completely Balanced Selection prevails for very many generations in succession. It is still certain that long-continued Independent Selection gradually passes into diversity of Selection producing divergent evolution.

(3) Though in more than one passage Darwin maintains that uniformity of external conditions involves uniformity of Natural Selection, and that isolation can have no effect in transforming a species if physical conditions and surrounding organisms remain the same, still, I think, that if the question had been distinctly brought before him, he would have admitted that exposure to a new or changed environment was not a necessary condition for change in the character of Sexual Selection. Now I think it can be shown that, besides Sexual Selection, there are several forms of Selection that depend upon the relations of the members of one species to each other, and that may undergo change without the organism being exposed to either a changed or a different environment.

Selection depending on the relations of the organism to the environment I call *Environal Selection*, of which I find two kinds, namely:—Natural Selection and Artificial Selection. Selection depending on the relations of the members of a species to each other I call *Reflexive Selection*, the chief forms of which I call Conjunctional, Dominational, and Institutional Selection.

(4) It must be carefully noted that Diversity of Selection depending on diversity in the relations of the organism to the environment, does not necessarily involve the exposure of the organism to different environments. In other words, change even in Environal Selection does not necessarily involve either change in the environment or the entrance of the species into a new environment. It may be due to a change in the methods of appropriating the resources of the environment, introduced by the organism without any change in the environment. Darwin's teaching seems, at times, to be in conflict with this statement, but there are passages in his writings which distinctly state that

variations in instinct may lead to different habits of sustentation, and it is evident that, as soon as the qualities that win success in the different sections differ, the Natural Selection must differ.

It should be remembered, however, that the meaning of anyone's statements on this subject will depend on his definitions of the words used. What is meant by environment, external conditions, and other similar terms? Until we define we shall only beat the air, however exact our statements may be. I therefore repeat what I have elsewhere stated, that, according to my definition, change in the environment is always change in activities that lie outside of the species, or of the segregated group of individuals that is under consideration. In Darwin's usage, the phrase "Change in external conditions" seems to carry the same meaning; but in some places this can hardly be the case, and accordingly great obscurity hangs over some of his statements on the most important subjects.

Diversity in the uses to which different sections of one species put their powers, when appropriating resources from the same environment, must produce diversity in the forms of variation that are most successful in the different sections. This I call *Active Natural Selection* as contrasted with *Passive Natural Selection*, which varies according to differences in the environment. All diversities of Natural Selection that do not vary according to differences in the environment must be classed as diversities of Active Natural Selection, for they must have originated in some variation in the powers of the organism, or in the diversity of uses to which it has put its powers. Diversity in the successful use of the powers of the species, whether initiated by diversity in the action of the species in its different sections, or by diversity in the activities of the different environments, necessarily introduces diversity of Natural Selection. This principle may be expressed as the *Dependence of Diversity of Adaptational Selection on Diversity of Successful Use.*

(5) Now diversity in the successful use of its powers in the different sections of a species cannot be maintained and accumulated without some degree of Segregation between the different sections, for within one intergenerating group every initial divergence is speedily merged in the general character of the group. This law may be briefly defined as the *Dependence of*

Increasing Difference in the kinds of Adaptational Selection on the Continuance of Segeneration. As was shown in my paper on "Divergent Evolution through Cumulative Segregation," without the aid of causes preventing intercrossing the selection of other than average forms will produce *transformation*, but never *divergence*,—will produce Monotypic, but never Polytypic Evolution.

(6) Diversity in the character of the Selection may be introduced, not only by the intervention of new forms, but also by the cessation of old forms of Selection. We shall find that important differences of this kind may arise, resulting in considerable transformation before any new form of Selection has distinctly supervened. A good illustration of the *Cessation of Selection* is found in the increasing frequency with which human mothers, notwithstanding their failure to give suck, succeed in raising their children. The power to give suck is through this process being diminished in the more civilized races, though there is no reason to believe that those who do not give suck have, on the whole, any advantage over those who do. The new result is therefore being produced, not by the introduction of a new form of Filio-parental Selection, but by the cessation, or the weakening, of an old form. Romanes was, I believe, the first to point out the effects that must often be produced by the cessation of Natural Selection *, but he has not considered the cessation of other forms of Selection.

(7) It is often convenient to distinguish between Selection resulting from rational devices and that resulting from the superior success of organisms better adapted than their rivals of the same intergenerant to the natural laws and conditions of the environment, or to the natural constitution of the species to which they belong. The former I call *Rational Selection*, and the latter *Adaptational Selection*. Under the former I place Artificial and Institutional Selection, and under the latter I place processes that are as unlike as Natural and Sexual Selection. This classification does not, however, seem to me so important, or so fundamental and clearly definable, as that which

* See an article on "The Factors of Organic Evolution" in 'Nature,' vol. xxxvi. pp. 402–404, in which reference is made to previous papers in which the Cessation of Natural Selection is discussed.

rests on the fact that some forms of Selection depend on the relations in which organisms stand to the environment, while others depend on the relations in which the members of the same species stand to each other. It may here be noted that Artificial Selection is the exclusive generation of those that are better fitted to the rational environment, through the failure to propagate of those that are less fitted. The effect is the same whether the failure to propagate is through lack of adaptation to human purposes, or through lack of adaptation to the unreasoning environment. Natural Selection is propagation according to adaptation to the Natural environment, and Artificial Selection is propagation according to adaptation to the Rational environment.

(8) Another discrimination which I have found it convenient to make, is that between Comparative and Superlative Selection. *Comparative Natural Selection* is the direct result of varying degrees of adaptation to the environment, without the additional influence of rivalry between the members of the same species. It is propagation of the fitted, according to the degrees of their fitness, controlling the expansion of a species before its members crowd and supplant one another. *Superlative Natural Selection* arises from the competition of members of the same species for the possession of identical resources, and results in the survival of those only that are most perfectly fitted to the environment. Comparative Selection is the Survival of the Fitted—of all the fitted, according to their degrees of fitness; Superlative Selection is the Survival of the Fittest—of only those who through superlative fitness can, in a crowded community, find the sustenance and other conditions necessary for perpetuating their kind.

The following classification (p. 329) of the forms of Selection will, I think, be a help in maintaining these and other distinctions.

FORMS OF SELECTION.

	ADAPTATIONAL SELECTION.	RATIONAL SELECTION.
ENVIRONAL SELECTION.	*Natural Selection.* Balanced. Unbalanced. Active. Passive. Comparative. Superlative.	*Artificial Selection.* Balanced. Unbalanced. Active. Passive. Comparative. Superlative.
REFLEXIVE SELECTION.	*Conjunctional Selection.* Balanced. Unbalanced. Sexual. Social. Filio-parental. Comparative. Superlative. *Dominational Selection.* Balanced. Unbalanced. Sustentational Domination. Protectional Domination. Nidificational Domination. Nuptial Domination.	*Institutional Selection.* Balanced. Unbalanced. Ecclesiastical. Military. Sanitary. Penal. Comparative. Superlative.

Natural Selection.—As Natural Selection involves not only the superior propagation of the better fitted, but the inferior propagation of the less fitted, and the non-propagation of the least fitted, it may be described as the *Exclusive propagation of those better fitted to the natural environment, through the failure to propagate of the less fitted.* Transformation by means of Natural Selection depends on varying degrees of adaptation to the environment in creatures that are intergenerating, the higher degrees being possessed by other than average forms. Divergence is produced by Natural Selection only when to the above conditions producing transformation are added causes that prevent intercrossing between the sections that are being independently transformed. In other words, *Independent Natural Selection produces Divergence.*

Sexual Selection is the exclusive propagation of those better fitted to the sexual constitution of the species through the failure to propagate of the less fitted. In the words of Darwin, "It depends on the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction." * It is the form of Reflexive Selection which has received Darwin's attention, and is consequently familiar to all. There are, however, certain points that need to be emphasized.

This is the principle in accordance with which correspondence is secured between the external characteristics and the sexual instincts of a species, and also between the instincts of the two sexes, in as far as they relate to reproduction. This result is secured partly by the failure to propagate of those whose powers of attraction and conquest do not reach the standard demanded by the instincts of the other sex, and partly by the failure of those whose instincts diverge too widely from the typical characteristics of the other sex. For example, on the highlands of North China I have observed a species of creeping cricket of the genus *Bradyphorus*, the male of which calls the female by a sharp stridulation, to which the female responds by approaching the male and finally climbing upon his back. Now we can well understand that the call of the male has been brought to its present shrill, penetrating perfection through the failure to attract mates in the case of males that were but feebly endowed; but it is equally certain that those females whose sluggish instincts have been capable of responding only to an unusually intense call have, for the most part, failed of leaving offspring, and, if any have been so unreasonable as to wait for the male to seek them out, they have, doubtless, perished without perpetuating their perverted instincts. If my view is correct, the change producing divergent sexual characteristics may be either in the instinct, or in the characters with which the instinct is correlated. It seems probable that in the vast majority of cases the more strongly divergent forms have been reached by a multitude of deviations alternating between the psychical and the physiolc-

* 'Descent of Man,' 3rd page of Chap. VIII.

gical and morphological characters of the species, the chief, indispensable condition being the prevention of interbreeding between the diverging sections of the species.

Sexual Selection is sometimes referred to as if it were the influence of sexual instincts in giving character to the organs of a given sex, first by the instincts of the same sex rousing the organs to successful activity in securing propagation, the degree of success depending on the degree of adaptation of the organ to the purpose of the activity (as in the case of barnyard cocks winning partners by the use of their spurs), and, second, by the instincts of the opposite sex being roused to successful action according as the endowments of the given sex are fitted to the end (as in the case of peacocks winning partners by the display of ornamentation). Starting, however, with this conception of the nature of Sexual Selection, we shall find great difficulty in obtaining from the principle any explanation of the origin of species, or of divergent evolution of any kind. If divergent instincts are the causes of divergent forms, colours, and qualities, what are the causes of the transformation of the instincts in lines that are persistently divergent? The problems of transformation and divergence are as far from solution after the application of the theory as before.

If, on the other hand, we recognize Sexual Selection as the harmonizing of the forms, colours, and qualities of a species with its sexual instincts, and of the sexual instincts with its forms, colours, and qualities, we shall not claim that either set of characters is directly and continuously the cause of transformation in the other; but rather that the two sets play upon each other in such a way as to produce a state of unstable equilibrium in both sets, the result of which is indefinite transformation in the secondary sexual characters of each section of a species that constitutes a separate intergenerant; and that the Independent Transformation inevitably results in Divergence. In Darwin's presentation of the principle of Sexual Selection, the chief endeavour is to show that differences in voice and ornamentation between the males and females of the same species are probably, in a large degree, due to diversity in the action of Sexual Selection upon the different sexes; but this is a very different result from differences in the same respects between those of the same sex in closely allied varieties and species; and no clear understanding of the subject will ever be reached till those who study and discuss the subject discriminate between these two classes of phenomena. The formation of differences of the former kind is simple transformation without divergence, while the entrance of differences of the latter kind is divergent evolution tending to the production of separate species.

If a species deficient in secondary sexual distinctions, after being divided into segregated sections, attains a high development of such distinctions, it is easy to believe that they will be developed in different ways in the different sections, and that thus they will become specific distinctions; but it is not so easy to see why a species in which sexual distinctions have already been fully developed should undergo divergent changes in the different sections into which it may be divided. It is in such cases that we discover the important influence of what I have called unstable equilibrium. It seems probable that in some cases small differences originating through indefinite variation in only a few isolated individuals are seized upon by the exaggerating fancies of the other sex, and are thus first preserved through isolation and then exaggerated by Sexual Selection. In other words, *Independent Sexual Selection produces Segregation and Divergenee.*

Social Selection is the exclusive breeding of those better fitted to the social constitution and instincts of the race through the failure to breed of those less fitted. Social organization has reference chiefly to co-operation in securing sustentation and defence. If for each species there were but one possible form of social organization through which sustentation could be secured, there would be no need of considering Social Selection, for the form of social organization would be rigorously determined by Natural Selection, and the success of the individual through conformity to that organization would be sufficiently explained by the principle of Natural Selection. But different forms of social organization are often exhibited by the same or closely allied species; and we find that, in such cases as elsewhere, the prosperity of the individual is largely dependent on his conformity to the social organization to which he belongs. Social Selection must, therefore, in some cases have been an important factor in maintaining a correspondence between the capacities and the social organization of a race or species. When a species or a section of a species is undergoing a change of social habits, there will be individuals that fail through reverting to the old instincts and methods which put them out of accord with the rest of the community. But through the failure of these the inherited instincts of the race are brought into increasing accord with the new habits till, in the case of most species, there are but few individuals that fail through lack of appropriate social instincts. Nevertheless in the branches of the human species that have attained the highest civilization the process is still far from complete, for the instincts of many individuals are in conflict with civilized habits.

We find that the natural faculties that are best fitted to secure individual success, and a numerous and long-continued descent, are different under different forms of civilization. Social habits in a great measure determine the food and clothing of a community, and thus deeply affect the qualities of the race. The exposure to which the young are subjected is also largely determined by social custom, and so the quality of the constitution that is permitted to survive. In other words, the form of Parental Selection that prevails in any community is often determined by Social Selection, as the form of Social Selection is sometimes determined by Natural Selection. Many matters, which amongst irrational animals are determined by instincts guiding the individual directly to the needed resources and showing what provision must be made, are with man determined by social instincts leading the individual to follow the general experience or traditional habits of his clan.

As in countries where there are no beasts of prey the gregarious instinct of cattle ceased to be a necessity for the preservation of life, it is no longer maintained by Natural Selection, but it may be preserved by Social Selection; for though occasional stragglers appear, they are, through lack of adaptation to the social organization, specially liable to fail of finding mates, and therefore to fail of propagating their kind. Between the capacities of a community and its social organization there is a constant action and reaction which tends with more or less rapidity toward transformation; and this tendency is increased when a small community, during a long separation from other communities, gradually increases in strength, independently constructing a civilization of its own. In other words, *Independent*

Social Selection tends toward divergent evolution of capacities and of social organization.

Filio-parental Selection is the exclusive breeding of those better adapted to the relations in which parents and offspring stand to each other, through the failure to live and propagate of those less adapted. How the power of giving suck and the corresponding instinct for sucking were first developed it may be impossible to tell; but it is evident that having once been established as the method of sustentation for the young of mammals, any young lacking the instinct would perish without leaving descent. There is every reason to believe that, with the exception of man, it may be truly said of every individual mammal that all its ancestry, through all its generations that have elapsed since they became fairly mammalian, have had this instinct in full force; and yet it sometimes fails, and the line of descent is cut short. Till comparatively recent times the same was true of man; but we now find some cases in which the young survive in spite of their inability to suck, and the constancy of this mammalian characteristic is being gradually impaired. There is also in some races an increasing tendency to shorter periods of lactation, or to the entire suppression of the function; so that it seems not improbable that there may yet arise a variety of the human species in which the power will be comparatively obsolete. Under such conditions the instinct for sucking would cease to be of any advantage, while special advantage would accrue to those best able to thrive on the artificial food habitually provided by the parents. In some countries this would be the milk of ruminating animals, while in other countries it would be some vegetable preparation. In the islands of Micronesia it is the sap that exudes from the cut end of the immature fruit-stalk of the cocoa-nut tree. In Japan it is a sweet extract of malt. Through this diversity in the food provided by parents for their infants and small children, there is even now a constant diversity in the Parental Selection prevailing in different countries. Diversity in the forms of Parental Selection is also produced by diversity in the clothing and artificial heat provided by parents, in the protection, on the one hand, of children from the wind and rain and direct rays of the sun, and, on the other hand, their exposure to the same with shaven heads or naked bodies, and in the methods of binding, cramping, and mutilating the head, feet, waist, and other parts of the body. From this point of view we see how largely the form of Parental Selection is determined by social custom, and how it is sometimes enforced by Social Selection, which excludes from the benefits of the caste or tribe all who have not been through the ordeal.

As Filio-parental Selection is due to different degrees of adaptation between the parent and offspring, it may be characterized not only by fatal departures in offspring from the characters required in their relations to their parents, but by fatal departures in parents from the characters required in parents in their relations to their offspring. As an example of the former, we may refer to the death at birth of children with excessively large heads; and as an example of the latter, to the death at birth of all the children of a mother with a contracted pelvis.

Dominational Selection.—Variations that are equally fitted to cope with the environment may be divided into two classes—those better able, and those less able, to cope with other members of the species in appropriating resources. Increase of population and the consequent competition between members of the same species condemns the latter to premature death, or at least to failure in propagating, unless they find new resources by migrating or by changing their habits. Competition between kindred for the possession of identical resources we find directly connected with three quite distinct principles of evolution:—(1) With the principle of *Superlative Selection* tending to the destruction of all forms except those most fully adapted to the environment; (2) With the principle of *Dominational Selection* tending to discriminate between those equally adapted to the environment, through the success and consequent propagation of those only that are best able to cope with their kindred in appropriating advantages; (3) With the principle of *Competitive Disruption,* tending to break up old relations and old habits, and so preparing the way for the formation of new habits producing segregation and divergence. Of these three principles, the last was referred to in the second chapter of my paper on "Divergent Evolution through Cumulative Segregation," p. 221, and the first has already been mentioned in this paper. The remaining one I shall here briefly describe, without attempting to show its important influence on the transformation and divergence of species.

Dominational Selection is the exclusive breeding of those better able to appropriate natural resources, or mates, or the provision made by parents or society, not through being better fitted to the environment or to the organized methods of co-operation and assistance, but through being better able to overcome or outdo their rivals of the same species. It results from the contest or rivalry with each other of members of the same species that are equally fitted to the environment and to the constitution of the species, and the consequent failure of all that are not able to cope with their kindred. "The law of battle" is a form of Dominational Selection which Darwin emphasizes as having great influence in determining what males shall have the best success in procuring mates. But there is a similar law determining what individuals shall obtain the resources furnished by nature, or elaborated by parents and society. We may have Dominational Selection relating to sustentation, protection, and nidification, as well as to the possession of females. And in gaining a single end there may be a great variety of dominating methods. Combat between males for the possession of females is not found in the vegetable kingdom; but the prepotence of the pollen of certain flowers over that of other flowers of the same race may play a similar rôle.

Dominational Selection differs from Natural Selection in that it does not depend on degrees of adaptation to the environment, and from other forms of Reflexive Selection in that it depends on a quite distinct form of the relationship in which members of the same species stand to each other. It seems desirable that this form of selection, which depends on adaptation for overcoming, outdoing, or supplanting others of the same species, should be clearly distinguished and named. We further note that there can be no doubt that Dominational Selection acting for many generations on sections of a species that are prevented from intercrossing will in all probability follow somewhat different lines. In other words, *Independent Dominational Selection will produce divergent evolution.*

Institutional Selection is a form of exclusive breeding closely related to Social Selection, but differing from it very much as Artificial Selection differs from Natural Selection. Institutional Selection is the influence of institutions, customs, and laws in determining what classes of individuals have an opportunity to marry and raise children. In most civilized countries criminals convicted of important offences are so confined as to prevent their adding to the population of the community during the time of their confinement. This is a method of improving the race that might be carried further than it has been. In some countries the insane are confined in asylums and not allowed to marry; and in other countries ecclesiastical and military restrictions prevent certain portions of the community from raising families.

Result of the foregoing Survey of Selectional Intension.

The analysis which we have now completed enables us to see how far changes in the form of Selection are due to changes in the environment, and how far to changes in the organism. We find:—First, that all the forms of Reflexive Selection are due to the relations of members of the same species to each other, and are liable to change without any change in the environments. Second, that Active Natural Selection is due to change in the successful use of the powers of the organism in dealing with the environment, and is not dependent on change in the environment. Third, that Passive Natural Selection, which is due to the exposure of the organism to a different environment, is often produced by the organism's entering a new environment without there being any change in either the new or the old environment. Fourth, that when Passive Natural Selection is produced by change in the environment, the more effective forms of Selection do not appear till the organism has so multiplied as to produce what I call Superlative Natural Selection through intense competition between rival individuals of the same species in gaining possession of limited resources. And, fifth, that Passive Comparative Natural Selection, which depends on change in the environment, without special rivalry between the members of one species, also depends on variation in the adaptations of the organism, many of which variations do not depend on that change in the environment which has produced the change in the Natural Selection, nor, indeed, on any change in the environment except those fundamental physical changes by which the world has passed from its primitive gaseous to its present partially liquid and solid state, rendering it a fit abode for organisms.

ELIMINATIONAL INTENSION.

Eliminational Intension is Segregation and divergence produced by the indiscriminate destruction or failure to propagate of part of the individuals of similar sections of a species. Though indiscriminate destruction cannot be classed as a form of Natural Selection, it may nevertheless be the cause of transformation; and when a species is distributed in sections that are prevented from intergenerating, divergent evolution will often be hastened by the indiscriminate destruction of part of the members of one or more of the sections. If a species inhabiting a large island is divided by geological subsidence into two equal sections, there may be a very close resemblance in the average character of the two sections; but if a subsequent eruption of hot ashes destroys a large portion of the individuals of one section, or of both, the probability of a close correspondence in the average character of the two sections will be very much less than before the eruption.

Again, when an area occupied by a species is divided into two or more equal districts, the occupants of which can have little or no opportunity for crossing, divergent evolution will arise in the different districts unless there is some constantly operating cause that ensures all the varieties that survive and propagate in any district shall survive and propagate in all the districts. No such cause has ever been pointed out; but, on the contrary, it can easily be shown that the probability is very small that such a correspondence would occur, even if at the time of the division of the area every individual in each district was represented by a completely similar individual in each of the other districts. Let us suppose a case:—

1. Suppose the creatures under consideration to be a species of mollusk, the sexual instincts of which act without any segregative tendency between the varieties of the same species, there being no aversion or other impediment that interferes with the free crossing of all the variations occurring within the limits of one district.

2. Suppose that the number of individuals in each district is 10,000,000.

3. Suppose that one in a thousand of these had a tongue strong enough to feed on the bark of the tree, the leaves of which are the ordinary food of the species, and that one in a thousand is capable of digesting the same, so that, in each district alike, one in a million could survive in this way though the crop of leaves should fail.

4. Suppose that there are, through diversity of adaptations of this kind to the products of the environment, ten different kinds

of accessible forms of food, on each kind of which one in a million of the individuals of each district might feed if driven by necessity.

5. Now suppose the same necessity should occur in each district through the destruction of the leaves on which they habitually feed; and that there are accordingly in each district a hundred survivors able to maintain themselves on other kinds of food.

Under such circumstances (the correspondences of which we have in our supposition made much more exact than the actual deviations from a mean ever present)—but even under such circumstances of completely parallel variation—what is the probability that in each of the separate districts the few that would meet with other individuals and have an opportunity to propagate the species would be similarly endowed and similarly related to the environment?

In order to still further simplify the problem, let us assume that in the case of each kind in each district the probability that it will succeed in propagating is exactly balanced by the probability that it will fail. The probability, then, that any given number of the ten kinds in a given district will succeed is found by estimating the number of combinations that can be secured by taking that number of things out of ten things in different ways. This is completely parallel to the number of ways in which ten pennies can be arranged as to head and tail, each penny representing one form of variation, and its lying head-up indicating success in propagating. In 1024 experiments the probability is

That 0 will succeed	....		1 time
„ 1 „ „	$\frac{10}{1}$	=	10 times
„ 2 „ „	$\frac{10\times9}{1\times2}$	=	45 „
„ 3 „ „	$\frac{10\times9\times8}{1\times2\times3}$	=	120 „
„ 4 „ „	$\frac{10\times9\times8\times7}{1\times2\times3\times4}$	=	210 „
„ 5 „ „	....		252 „
„ 6 „ „	....		210 „
„ 7 „ „	....		120 „
„ 8 „ „	....		45 „
„ 9 „ „	....		10 „
„ 10 „ „	....		1 „

These figures are found in the eleventh line of what is known as the "Table of the Binomial Coefficients," or the "Arithmetical Triangle"*. And so in the case of any number of objects, the number of combinations that may be made with n objects is found in the $n+1$th line of the Arithmetical Triangle classified according as there are 0, 1, 2, 3, or more objects in each combination. The whole number of combinations may also be found by calculating the nth power of 2.

The possible combinations of the ten varieties in question are 1024, which is equal to 2 raised to the 10th power; the probability, therefore, that the combination that succeeds in one district will also succeed in the other district is $\frac{1}{1024}$, or 1 in 1024; while the probability that those that succeed in the one district will not be all the same as in the other will be $\frac{1023}{1024}$, or 1023 in 1024, which is more than a thousand times greater than the reverse probability.

These 1024 different results, any one of which may occur in one section, are calculated on the supposition that all the representatives of the species in one section that succeed in propagating will in time coalesce by intercrossing; but, as we shall presently see, the number of divergences in the two sections may be vastly increased by the diversity of ways in which the same varieties may be combined through the greater or less influence of minor segregations within the bounds of each district.

Amalgamational Intension.

In my paper on "Divergent Evolution though Cumulative Segregation," p. 233, I have referred to the fact that the vast majority of divergent forms produced by Segregation, after existing for a time, are interfused with competing forms of the same species. Now it is evident that when a permanent Segregation arises, if in the separate sections there is a diversity of amalgamations between the slightly divergent forms produced by partial segregations, the results will be divergent in these separate sections. That there will be diversity in this respect, we may argue: first, from the improbability that all the varieties in one section will occur in each of the other sections; second, from the improbability that if the same varieties occur in each section, they will occur in the same proportions; and, third, from the improbability that if they are the same and in the same

* See 'Principles of Science,' by W. S. Jevons.

proportions, they will break over their barriers and interfere with each other in precisely the same way in each section. Amalgamational Intension relates only to the last point. The other two points have been discussed under the principle that Separation always involves more or less Segregation (see the third paragraph of this paper).

Taking up again the supposed case considered under Eliminational Intension, if the different kinds of new food were so situated as to make it more or less difficult for those feeding on one kind to cross with those feeding on other kinds, the representatives of the species in each of the completely separated districts would be divided into minor segregations of a partial kind; and the different degrees of intercrossing between the minor segregations in the separate districts would be an additional cause of divergence, which we may appropriately class as a form of Amalgamational Intension. Occasional interchange of stations by the varieties in one district would produce a degree of homogeneity in the forms of one district that would not be found when comparing those of different districts; but as the degrees of intercrossing between any two or more identical varieties that might happen to be preserved in both districts would, in all probability, differ in the different districts, the correspondence that at first existed between certain portions of the two sections would gradually disappear. We shall find that in order to ascertain with facility the number of different sets of combinations in which any given number of varieties may be combined while all are propagating, and the probability that any given degree of correspondence will present itself in any two sets of combinations that may be taken at random, we need a table by which the number of permutations that may be made with given numbers of things may be analyzed. I have constructed such a table, which I call the Permutational Triangle *, with the aid of which the solutions of problems that would otherwise require much time are easily reached.

Returning to the above calculation, we observe that in 1024 experiments, under the circumstances there assumed, there would probably be but one occasion in which, out of the ten identical varieties which were assumed to occur in each district, the same varieties would succeed in propagating in each district. We

* I give in an Appendix this Permutational Triangle, calculated to the tenth line, with an explanation of how it was formed.

have now to consider the degree of probability that these identical varieties will make the same combinations with each other in the different districts. I shall not attempt to give a complete answer; but by carrying the computation through several steps, I shall sufficiently exhibit the extreme improbability that, even when identical varieties succeed in propagating in the different districts, they will combine with each other in the same way and in the same proportions.

As in the case of the 10 varieties that have been under consideration, 5 is more likely to be the number of varieties that succeed than any other number, 5 is most likely to be the number of successful varieties in each district when the varieties happen to be the same in each district; and we will therefore begin with that number. If, now, we suppose that there are 5 varieties in each district, and that there is the same chance in the case of each variety that it will breed with any one of the other varieties, as there is that it will be segregated and breed by itself, we shall find that in 120 experiments there will probably be 1 occasion in which all the varieties of one of the districts will be segregated from each other, and 10 occasions in which three of the varieties will be segregated, and 20 occasions in which two will be segregated, and 45 occasions in which one will be segregated, and 44 occasions in which none will be segregated *. These probabilities are expressed by the fractions $\frac{1}{120}$, $\frac{10}{120}$, $\frac{20}{120}$, $\frac{45}{120}$, and $\frac{44}{120}$. And the probability that the same varieties will be intercrossed and the same ones segregated in each district is $\frac{1}{120}$; while the probability that some one particular set of segregations and intercrossings that is designated in advance will occur in both districts is $(\frac{1}{120})^2$. For example, the probability that all the 5 varieties in one district will be segregated is $\frac{1}{120}$; and the probability that all in both districts will at the same time be segregated is $(\frac{1}{120})^2$.

But the two districts may correspond by the complete failure of all varieties to propagate, in which case they will continue to correspond. Again, there may be but one variety in each district that succeeds in propagating, and that the same, in which case there will be no chance for diversity of Amalgamation in the different districts, at least not before a diversity of subordinate segregations has first arisen. Again, if the same two varieties

* These figures are found in the 5th line of the Permutational Triangle. See Appendix.

succeed in propagating in each district, the probability of complete correspondence in integration will be as 1 to the factorial of 2, or as $\frac{1}{1\times 2}=\frac{1}{2}$;

if the same 3 varieties, the probability $=\frac{1}{1\times 2\times 3}=\frac{1}{6}$;

„ „ 4, the probability $=\frac{1}{1\times 2\times 3\times 4}=\frac{1}{24}$;

„ „ 5, „ $=\frac{1}{1\times 2\times 3\times 4\times 5}=\frac{1}{120}$;

„ „ 6, „ $=\frac{1}{720}$;

„ „ 7, „ $=\frac{1}{5,040}$;

„ „ 8, „ $=\frac{1}{40,320}$;

„ „ 9, „ $=\frac{1}{362,880}$;

„ „ 10, „ $=\frac{1}{3,628,800}$.

These fractions represent the probability of complete correspondence as to the varieties that intercross and those that remain segregated in the different districts when the same varieties occur in each district; and the squares of these fractions represent the probability that any special combination that may be indicated will occur in both districts at the same time. If there are, for example, the same ten varieties in each district, the probability that they will combine in the same way is $\frac{1}{3,628,800}$, and the probability that this way will be the breeding of each variety with its own kind, without any intercrossing, will be $\left(\frac{1}{3,628,800}\right)^2$. But there may be degrees of correspondence in the combinations of different districts. As we have just seen, the probability that there will be correspondence in ten points is $\frac{1}{3,628,800}$, that there will be in eight points is $\frac{45}{3,628,800}$, that there will be in but one point is $\frac{1,334,960}{3,628,800}$, while the probability that there will be no correspondence is $\frac{1,334,961}{3,628,800}$ *.

We have thus far considered only the divergences that come

* The denominator of these fractions is the factorial of ten, that is $1\times 2\times 3\times 4\times 5\times 6\times 7\times 8\times 9\times 10$, and the numerators are found in the tenth line of the Permutational Triangle. See Appendix.

from a diversity of binary combinations coexisting with segregated varieties; but it is evident that the number of divergent arrangements that may be produced by any given number of varieties exceeding two will be much larger if to the above arrangements are added all that may be produced by arranging single with trinary, and binary with trinary; and if more complex combinations are introduced, the number may be still further increased.

Of the five suppositions with which we started*, the second and third assume a uniformity in the contingencies relating to the number and character of the individuals never realized in the different sections of a species that is divided by natural barriers; and the fifth assumes a uniformity in the changes affecting the environment which, though not often realized, is here assumed for the sake of showing that divergence of character is not dependent on the organism being exposed to different environments. In connection with the fourth supposition, it would have been in accordance with the usual conditions of nature to have assumed that, besides the many kinds of food of which only a very small fraction of the species could avail themselves, there would be a few kinds on which much larger numbers could feed; and that when the numbers that could partake of one kind of food were sufficient to ensure the propagation of those thus adapted, that variety would survive in both districts. But such certainty relating to the propagation of some of the varieties would not prevent the contingencies and the divergences that would arise in the propagation of the much rarer or less favoured varieties. It is also evident that similar contingencies would arise whenever the pressure of population on the supply of food should render it necessary for large numbers to seek new resources. The divergent tendency of such pressure, from whatever cause the pressure arises, is in no respect an arbitrary supposition; and the arbitrary assumptions which I have introduced in order to simplify the problem remove from consideration some of the contingencies that must produce still greater divergence.

Fecundal Intension,

or *Segregation and Divergence produced by Independent Fecundal Transformation*, that is by different relative degrees of fertility

* See page 338 of this paper.

possessed by the same forms of variation in separate sections of the species.—Relative Fecundity is propagation according to degrees of fertility. As it involves not only the superior propagation of the more fertile, but the inferior propagation of the less fertile and the non-propagation of the least fertile, it may be described as the exclusive propagation of the more fertile, through the failure to propagate of the less fertile. It would avail nothing in determining the form that is to prevail in succeeding generations if it did not in some degree preclude the crossing of the less fertile with the more; but, as it is evident that, so long as increased fertility is not a disadvantage, the more fertile half of the species will leave a larger number of offspring than the less fertile half, it follows that when the offspring have come to maturity a larger portion of the fertile will consort with the fertile than in the previous generation, and so the fertility of the following generation will be still further increased. The chief check to this law of *Cumulative Fertility* is found in the antagonistic law of Cumulative Adaptation through Adaptational Selection. The combined action of these two laws results in the triumphant development of the most fertile of the best fitted, or the best fitted of the most fertile.

Another result from the combined action of these two laws is that in species that are well adjusted to the environment the typical, that is the average, form of the species is not only the best adapted, but it is the most fertile; and this correlation between fertility and adaptation in the average form of the species or race is a strongly conservative principle, tending to prevent the rapid transformation of the race or species. Giants, dwarfs, and extreme departures from the type of other kinds are more likely to be sterile than the typical form of the species; and therefore if, through change in the environment or in the social conditions, some extreme form has an advantage in gaining subsistence, it will usually fail of propagating its kind with the relative rapidity of the less-favoured average form. This is at present true of highly intellectual variations of civilized man. Those of moderate capacities are more prolific, and accordingly persist, though less successful in other respects than the intellectual. But so long as the most successful individuals are those surpassing the average in intellectual endowment, so long will the average endowment be more or less steadily advancing; for, of intellectual families, those that are fairly fertile will leave more impress on succeeding generations than those that are sterile; and of fertile families, those that are above the average in intellect will have the best success in leaving descendants to inherit their endowments.

Combined Influence of these Principles.

We have not at present sufficient knowledge of the influence of each of the principles of transformation to enable us to estimate their comparative importance; but we know enough of their combined action to anticipate with confidence that wherever Separate or Segregate Generation arises, producing more or less divergence, there these principles will in time intensify the result. The transformations and divergences of nature are produced by the interplay of numerous factors most intimately combined, and though for the purpose of comprehending the process we are compelled to study each principle by itself, we must remember that in nature they not only combine, but combine in a vast variety of ways. There is, however, reason to believe that species sometimes become so devoid of plasticity that all transformation is precluded, and, if the environment is changed, even in the most gradual manner, extinction is the result.

Divergent Evolution in the Land-Mollusks of Oahu.

Oahu is one of the Sandwich Islands, or Hawaiian Islands as they are now usually called. It is of volcanic origin, but the two mountain-ranges, which lie one on the north-east and the other on the south-west side of the island, show no signs of recent volcanic action. Unlike the mountains of Hawaii and East Maui, their sides are very deeply furrowed by the action of water, and their forests are not broken by flows of lava. The forests of the island cover these two ranges, forming two disconnected strips, the one about 36 and the other about 18 miles in length. In these forests are found 600 or 700 varieties, representing over 200 species, belonging to 7 subgenera, of the subfamily *Achatinellinæ*.

Two of these subgenera, *Amastra* and *Leptachatina*, are, for the most part, found under the dead leaves of trees in damp places; and one, *Laminella*, is found chiefly on low shrubs, while the remaining four are always found on trees or shrubs. Now it must be remembered that the climate is tropical, and that the rainfall is so distributed through the year that in the shady groves there is nothing to drive the arboreal species from their haunts on the leaves or branches of the trees. Still further, as this branch of the Helicidæ, unlike most other branches, produces its young, not from eggs, but in a living active form, there is no occasion in its life-history that requires it to leave the tree in which it lives from generation to generation. In the distribution and divergences of these varieties and species we learn the following lessons :—

1. *Varieties are incipient species, and species are strongly pronounced varieties.*

A full collection of the varieties and species of any polymorphic genus produces an oppressive sense of confusion on the mind of any one who examines it for the first time. This is preeminently true of a full collection of the *Achatinellinæ* of the island of Oahu. Seven genera or subgenera are represented by a multitude of varieties and species, which, within the limits of each genus, are, for the most part, completely intergraded with each other. As natural selection has not removed the intermediate forms, it is impossible to say where a species begins and where it ends. Having selected a given form as the type of a given arboreal species, we soon find that it inhabits perhaps only one or two valleys, say half a mile in width, and only one, two, or three miles in length. Beyond these limits it is represented by varieties that become more divergent as the distance from the home of the type increases ; and, in the case of *Achatinella* and *Bulimella*, this divergence is so rapid that at the distance of 8 or 10 miles every one will admit that the forms all belong to different species. Indeed, in many cases, though the same vegetation is present, the habits of feeding have changed, while in other cases the form has changed while the habits remain essentially the same.

Though it is easy to find degrees of divergence which most naturalists will agree in calling specific, but which in a full collection are shown to be completely intergraded, yet if a full collection of the different forms should be submitted in succession to a hundred different naturalists to classify, it would be found that no two would agree as to the number of species ; and a still greater diversity of opinion would be revealed as to where the limits of the different species should be placed. This is exactly what we might expect if varieties are incipient species, and species are simply more strongly developed varieties. Such being the case, it is folly to ask that the nomenclature should be based on some fundamental distinction between species and varieties.

The best nomenclature is the one in which the specific distinctions correspond in degree with those that are recognized as specific in other families, and in which a degree of divergence that is considered specific in one part of a genus is considered specific in every part. If the distinctions on which Reeve, Pfeiffer, and Newcomb have founded the species in Makiki and Manoa are received as specific distinctions, then similar distinctions occurring in the forms of other valleys must be recognized as belonging to different species. I by no means contend that these differences should be regarded as specific; but having received the three or four forms of *Achatinella* found in Manoa as good species, it will not do to say that the three forms of *Achatinella* found in Waialei, differing from each other in the same way, are but one species.

Notwithstanding the diversity of opinion that will always exist as to how many species should be made of the forms occurring in any one valley, every one will agree that the forms of *Bulimella* and *Achatinella* found in any one valley are quite distinct species from those found in valleys that are ten or twenty miles distant. The lessons we are drawing from the divergences in this family are therefore not dependent on any special views concerning the number of species that ought to be received.

As examples of intergrading species, examine first the types of *Achatinella producta*, *A. adusta*, and *A. Buddii* from Makiki; then all the forms of these and the other species of *Achatinella* found in Makiki; and then the forms found in the successive valleys of the whole mountain-range.

If freedom from intergrading is received as the necessary and sufficient test of good species, then a multitude of forms that are now only varieties may be turned into good species by burning the forests in alternate valleys on either side of this mountain-range. Moreover, if this is the true test of species, the species-maker who throws intergade forms into the fire is quite consistent, even if not quite frank.

Whether we call these divergent forms species or varieties, the process by which the divergence has been produced is a matter of equal interest. Indeed, some evolutionists maintain that one of the chief desiderata in the theory of evolution is an explanation of the origin of varieties *. Variations are deviations from the average, but varieties are groups of individuals in which the averages differ, and in which the inheritable characters differ. Still further, it is usually admitted that the divergences presented by varieties are not always essential to the well-being of the forms that possess them, and that in many cases the forms that are confined to separate localities might exchange positions without suffering disadvantage. Divergence in these initial stages has seemed to many to be an obscurer problem than the advancing usefulness which sometimes entirely remodels an organ. For, as Prof. Le Conte has said, "Natural selection does not make an organ useful, but only more useful."

I believe that the theory of divergent evolution, presented in this and the preceding paper, is applicable to the formation of divergences during the stage when some of the differences, if not all, bring neither advantage nor disadvantage to those that possess them. Whatever we call these divergent forms, can we give any explanation of the causes that have produced them?

2. *Divergent Evolution does not necessarily depend on either change in or change of the environment.*

In other words, it does not necessarily depend on change in the conditions surrounding the organism, or on the organism being brought into a district presenting a different set of conditions.

Darwin maintains that isolation (that is geographical separation), without any differences in the surrounding organisms or in the physical conditions, presents no occasion for divergence of character. He says, "If a number of species, after having long competed with each other in their old home, were to migrate in a body into a new and afterwards isolated country, they would be little liable to modification" ('Origin of Species,' 6th ed. p. 319).

Spencer expresses the same idea by saying that "Vital actions remain constant so long as the external actions to which they correspond remain constant" †. "There must be maintained a

* See 'Evolution and its Relations to Religious Thought,' by Joseph Le Conte, published by Appleton & Co., page 252.

† Though apparently opposed to his theory of "the production of certain local forms by amixia," this same idea is found in Weismann's 'Studies in the Theory of Descent,' pp. 109–115 (English edition).

tolerably uniform species so long as there continues a tolerably uniform set of conditions in which it may exist." (See Spencer's 'Principles of Biology,' §§ 91, 156, 169, 170.) In other words, divergence of character in the descendants of one stock occupying different districts does not arise except as it is preceded by difference in the physical conditions, or in the surrounding organisms, of the different districts. After moulding this thought in many forms, Spencer makes it the fundamental principle on which he builds not a small portion of his philosophy. Darwin is more guarded in his statements; still, as we have already shown, he sometimes seems to reason from an assumption quite in accord with what Spencer would have us receive as essential to the very idea of causation in vital processes. For example, his explanation of the fact that on the different islands of the Galapagos Archipelago one genus is, in many cases, represented by several closely allied species which are undoubtedly modified forms of one continental species, seems to rest on the assumption that if every species that gained access to any island had at the same time gained access to the other islands of the archipelago, there would then have been no occasion or opportunity for the divergences we now find (see 'Origin of Species,' 6th ed. p. 355).

It seems to me that the divergences presented by the varieties and species of the subfamily *Achatinellinæ* of the Sandwich Islands are at variance with this assumption. Not only are islands in sight of each other occupied by divergent species, but different parts of the same mountain-range, exposed to the same winds and rains and clothed by the same vegetation, are the homes of divergent forms.

Turning to the map of the island of Oahu, we find a mountain-range extending 36 miles from north-west to south-east nearly parallel with the north-east coast. The north-east side of this range is exposed to the trade-winds fresh from the ocean, and accordingly receives a heavier rainfall than the other side; but there is not much difference in the amount of rain received by the different valleys on one side of the mountain. In nearly all these valleys on either side of the range are found shady groves of what the natives call the "kukui" (*Aleurites triloba*). Many species of the subgenera *Achatinella* and *Bulimella* have their haunts in these groves, some species clinging to the leaves and young branches, and others to the old branches and trunks. Most of the species thrive only where the shade is dense and the atmosphere laden with dampness a large portion of each month.

The student who starts with the assumption that divergent varieties and species arise only through exposure to different environments, will expect that these groves, at least those on the same side of the mountain-range, will be occupied by the same species. Having found one set of species in a given valley, when he comes to a valley ten miles distant possessing the same conditions of soil, rainfall, vegetation, and shade, where the birds, reptiles, and insects are the same, where the mice and ants, their only known enemies, are the same, he naturally looks on the leaves and branches of the familiar trees for the snails he has found in similar stations not far distant; but what is his surprise to find only different species, all allied to, but quite distinct from, those he has previously known! Twenty miles from the first valley he renews his investigations, finding the forms of all the different groups still more divergent, though all the conditions of the environment are, so far as he can observe, the same.

He finally perceives that he must either assume that there are occult influences in the environment varying with progressive force with each successive mile, or he must give up the theory that the cause of this divergence is exposure to different environments.

3. *When the environment is the same in two districts occupied by allied species or varieties, it is evident that the differences that distinguish the latter cannot be advantageous, even though their differences include strongly contrasted habits.*

For in order that these differences should be advantageous, it is necessary not only that they should relate to the performance of vital functions, and therefore be differences of adaptation, but it is necessary that these differences of adaptation should relate to differences in the environment, so that the forms would be at some disadvantage if they should exchange districts. Adaptational specific differences are not always advantageous, ard in such cases the divergence cannot be primarily attributed to diversity in the action of natural selection in the different districts. Under the protection of Isolation, diversity of natural selection may arise which helps in producing divergence; but when the environments are the same, the divergence is in no sense advantageous, and, in some cases, may even be disadvantageous.

A familiar example will perhaps put the distinction between the causes of existence and transformation and the causes of divergent existence and transformation in a clearer light. The forms of language are growths that are governed by the laws of utility as fully as the forms of varieties and species. Each language and each part of a language exists and persists only as it is found to be of use. The "Survival of the Fittest" is a law that is perhaps as conspicuous in the domain of language as it is in the organic world. Again, every language, like every organic species, is in many respects determined by the environment. A language, for example, developed in Java will present names for many plants and animals that will not be represented in a language developed in Greenland. But, granting all this, does it follow that linguistic differences are necessarily advantageous? The Polynesian system of counting by fours, and the Eskimo system that proceeds by scores, are undoubtedly useful systems; but is there anything advantageous in the difference? I think not, for each system is as well adapted to the environment of the other as to its own environment. We may look upon the more important parts of a language as persisting through their usefulness, the survival of the fittest being the law; but the divergent evolution which brings several languages out of one seems to be principally due to other principles which are closely akin to the principles that produce divergences in the organic world. The fundamental condition in both organic and linguistic divergence is Segregation; and, this being secured, diversity of habits, bringing diversity of aptitudes and diversity in the forms of survival, is sure to arise even when the environment is the same.

4. *Specific differences are not always differences of adaptation to the environment; and those that are not should not be attributed to the action of natural selection.*

It is admitted by every one that a distinction relating to a character that is of no use in the economy of the organism cannot have arisen under the influence of natural selection. Those who maintain that all specific distinctions are due to natural selection maintain at the same time that these distinctions are both adaptational and advantageous. There are naturalists who maintain that the very essence of the Darwinian theory is "that specific differences must be advantageous," and therefore adaptational; while they do not claim the same for generic, family, and ordinate distinctions, or indeed for varietal distinctions, if I rightly understand *. I have never seen any attempt to explain this supposed exception in the midst of the taxonomic series; and it seems to me that the break in the continuity of nature which this interpretation of the Darwinian theory supposes, should lead us to a very careful investigation of the facts before we accept it as a true interpretation of nature.

I shall content myself with pointing out one distinction, occasionally occurring between allied species, for which no use has ever been, or is likely to be, found. I refer to the distinction between what are known as dextral and sinistral forms. This distinction relates to the tortion of the animal and its shell upon itself. It is most easily recognized by placing the shell on its back with the aperture upward, and observing whether the aperture lies on the right side of the central columella of the shell or on the left. In the first case it is described as dextral, in the second as sinistral. In most families and genera of water-mollusks the sinistral form occurs only as a sport (amongst Mammals the heart is sometimes found on the right side), and even amongst air-breathing mollusks the dextral form vastly predominates. Amongst the *Achatinellinæ*, *Amastra* and *Leptachatina*, which are genera of terrestrial habits, are (with perhaps the exception of one or two species) dextral in form; while the other genera, which are plant-feeders and constantly hanging to branches or leaves, present many species that are constantly sinistral, and many others that are both dextral and sinistral. Why should *Achatinella adusta* in Panoa and Makiki be constantly sinistral, when its nearest allies found in the same valleys are both dextral and sinistral? Why should *Achatinella bacca* and *A. abbreviata* in Palolo and Waialae be constantly dextral when the other species of *Achatinella* in the same valleys are for the most part sinistral? Is there any adaptation to the environment possessed by a dextral form which would be lost if the form was reversed? If not, natural selection could not have anything to do with that part of its character. *Bulimella rosea* is sinistral, while *B. bulimoides* is dextral. If in this respect they should exchange forms, would

* See letter from Mr. W. T. Thiselton Dyer in 'Nature,' vol. xxxix. p. 8.

any disadvantage be experienced by either species? It is impossible to conceive of any disadvantage that would follow, and therefore I cannot believe that this difference in the two species is primarily due to natural, sexual, or any other form of selection.

There are many other specific distinctions presented in this family which seem to be of no advantage, though they are not so far removed from all suggestion of the possibility of use as the character we have just been considering. The brilliant colours and varied patterns presented by many of the arboreal species would be of advantage to themselves, if they served as warning of nauseous qualities to creatures that are liable to prey upon them; but no such creatures exist. The birds of the forest-region are exclusively fruit- and nectar-feeding, and the mice which in recent years have made sad havoc with the mountain snails, unfortunately do not spare the highly-coloured species.

There can be no doubt that when representatives of different groups or subgenera occupy the same trees they remain segregated through the influence of sexual instincts, which must be associated with some means of recognizing those of their own group; but it is not at all probable that the colours and patterns of any species are recognized by their mates, or have been developed under the influence of sexual selection. There is, therefore, strong reason to doubt whether selection of any kind has been concerned in the production of the beautiful colours and patterns of these species, unless possibly correspondences in colour within the limits of a genus are, in some cases, due to the inheritance of tendencies produced by selection when conditions were very different from what we now find. But the divergences in colour and pattern in the species of one genus cannot be thus explained.

5. *The average radius of distribution for species of the same value in different groups of closely-allied species varies in the different groups directly as the power and opportunity for migrating, and inversely as the plasticity and variability of the several groups.*

Comparing the distribution of the *Helices* of Europe with that of the *Achatinellinæ* of Oahu, the most striking contrast is found in the size of the areas occupied. *Helix pomatia* is distributed from England to Turkey, over an area two thousand miles in length, while of the seven genera of *Achatinellinæ* on Oahu

I know of but one species that seems to be distributed over the whole 36 miles of the main mountain-range, and this one is represented by three varieties belonging to different parts of the range and perhaps worthy to be regarded as different species. The species to which I refer is *Auriculella auricula* (Fér.), the typical forms of which are found on the eastern half of the mountain-range. On the other half of the range we find the closely allied forms to which I have given the manuscript names *solida* and *pellucida*. This great contrast in the size of the areas occupied must be due either to the greater plasticity of the Sandwich-Island species, or to their having inferior opportunities for migrating, or to both causes. As I become better acquainted with the great difference in the habits and circumstances of the contrasted species, I give increasing weight to the difference in the opportunities for migrating. With the continental species, floods must be one great means of distribution; but in the case of the insular species, the floods would carry floating individuals upon the grass-land or into the sea, in either case to perish. Again, the habit of travelling upon the ground, which belongs to most of the Helices of Europe and America, gives incalculable opportunities for migration which are not enjoyed by species that are strictly arboreal, as are many of the Sandwich-Island species. Most of the Sandwich-Island species are still further restricted in their opportunities by their inability to resist a dry atmosphere or exposure to the sun, which renders it necessary that they should remain in the isolated areas that are favoured with shade in the different valleys.

The habits of the different subgenera occupying Oahu are also instructive as throwing light upon the relative areas occupied by the species of the different genera. *Achatinella* and *Bulimella* seem to be the most restricted in their opportunities for migrating: first, because they are entirely arboreal in their habits, clinging to the trunks and branches of trees through their whole life-history; and, second, because, for the most part, they occupy the shady and damp thickets and groves, the shade in each valley being separated from similar shades in adjoining valleys by lofty and sparsely wooded mountain-ridges at each side of the valley and by open grass-land at the mouth of the valley. On the other hand, *Apex*, which for the most part occupies trees and shrubs on the ridges which are connected with each other through the central ridge of the mountain-range, and *Amastra* and *Lepta-*

chatina, which are for the most part found on the ground under dead and decaying leaves, seem to possess better opportunities for migration than either *Achatinella* or *Bulimella*. Corresponding with these facts we find the species of *Achatinella* and *Bulimella* especially limited in the areas they occupy, while the species of *Apex*, *Amastra*, and *Leptachatina* are less so. For example, the area occupied by *Amastra turritella*, *A. tristis*, and *A. ventulus* includes the areas occupied by many species of *Achatinella* and *Bulimella*; and *Apex loratus* and *A. pallidus*, occupying the mountain-ridges, range from Makiki to Halawa, exceeding the range attained by any arboreal species occupying the valleys of the same region.

6. *When a group of divergent forms that are fertile with each other are being developed through the influence of local or geographical segregation, other conditions remaining constant, the number of forms that will be produced within a given area will vary inversely as the square of the average radius of distribution for the different forms.*

As this average radius of distribution may be taken as the measure of the power and opportunities for migration, we may say that other powers and opportunities remaining constant, *the number of species developed within a given area will vary inversely as the square of the power and opportunity for migration.*

Though migration is in one sense a cause of isolation, it is evident that the number of isolated groups of individuals does not increase with the increase of migration. Isolation is produced by the great contrast between ordinary and extraordinary combinations of opportunities for migration; and this contrast is as great in the case of species that have limited powers and opportunities, as in the case of those that have very great powers and opportunities. The number of isolations thus produced that can exist within the limits of a given area must vary inversely as the square of the power and opportunity for migration.

The facts of distribution we have been considering seem to correspond to this law.

7. *Forms that are most nearly related, and are therefore the least subject to sexual and impregnational segregation, are distributed in such a manner that their divergence is directly proportional to their distance from each other, which is also the measure of the time and degree of their geographical*

segregation; while those that are most manifestly held apart by sexual instincts and impregnational incompatabilities do not follow this law.

Bulimella is represented by two groups of species, one of ovate form, the other elongated and with the outlines of the spire less rounded. The widest divergence between these groups is presented by species occupying the same districts and valleys, but the widest divergences in the species of either of these groups are found in valleys widely separated. In the latter case, the degree of geographical separation is probably an approximate measure of the time and degree of segregation, and therefore the measure of the degree of divergence; while, in the former case, the segregation is probably as complete between forms occupying the same valley as between those of widely separated valleys. There is reason to believe that in the eastern part of the island these two groups are not held apart by sexual segregation or segregate fecundity and vigour, for there is complete intergrading, and the divergence between the groups in any one valley is much less than is found in the north-west portion of the island, where sexual incompatibility seems to hold them apart.

Achatinella bacca and *A. abbreviata* completely intergrade with each other, but they are associated with a number of other species of *Achatinella* with which they do not intergrade, prevented it seems to me by mutual antipathy and sterility. We have, therefore, in the eastern valleys two groups of *Achatinella* completely segregated from each other, though occupying the same districts and in some measure the same stations; while in the other valleys the two groups coalesce, the different species occupying any one valley being only partially segregated by divergent habits of feeding

The different subgenera, which are undoubtedly segregated by divergent sexual instincts, as well as by physiological incompatibilities, are equally divergent, whether we compare forms from the same, or from distant valleys.

8. *The distribution of the varieties, species, and genera of* Achatinella *on this island is just such as would be produced by divergent evolution, which depends on segregation as a necessary condition even when the environments are different, and which always follows long-continued segregation even when the environment surrounding the different sections is the same.*

Increasing difference in the forms of natural selection does not necessarily depend on exposure to different environments, but does depend on some form of Independent Generation. It may be safely said of the multitude of varieties which inhabit the island of Oahu, that every one is more or less segregated from all other varieties. And I believe this will be found true concerning varieties in every part of the world. This fundamental fact would probably never have been denied, except for the delusive idea that the advantage of divergence would lead to the accumulation of divergence even if segregation were entirely wanting. What could be a greater mistake for the breeder of animals than to imagine that by selecting extreme variations and breeding them together he would in time secure well-marked races? It must be equally at variance with fact to suppose that any advantage secured by divergent variations can be preserved and accumulated while the different forms are freely intergenerating.

In the family we are considering, the chief forms of segregation are probably what I have called local, geographical, industrial, and sexual segregation, strengthened in many cases by segregate fecundity and vigour. As illustrating local segregation I would mention varieties and species of *Apex*, for the most part occupying the mountain-ridges which are all connected with each other, without the intervention of geographical barriers. Geographical segregation is illustrated in the forms of *Achatinella* and *Bulimella*, which for the most part occupy the deep valleys, the ridges forming barriers that are very rarely surmounted. Industrial segregation is illustrated by the closely-allied varieties of one group of species that occupy one valley, but are prevented from freely crossing by different habits of feeding. It is probable that sexual or seasonal segregation prevents the pairing of *Achatinella* with *Bulimella* when both occupy the same trees. Moreover, cross sterility would undoubtedly prevent the multiplication of the hybrids, if cross-unions ever do occur between forms so widely divergent. There can be no doubt that the same principles prevent the strongly marked groups of either genus from intergenerating; as for example, in the case of *Achatinella bacca* and *A. abbreviata*, which are intergraded with each other, but not with the surrounding species of *Achatinella*.

Again, divergent forms of natural selection do not necessarily depend on exposure to different environments. Industrial Segregation is produced by different methods of using the environments; and the same cause will often produce diversity in the forms of natural selection affecting the segregated sections. Cumulative divergence in the methods of using the environment in the different branches of the species depends upon their segregation, and, therefore, increasing divergence in the forms of natural selection affecting the different branches depends on their segregation. But Industrial Segregation is not the only form of Independent Generation that opens the way for increasing diversity of natural selection. Geographical Segregation under the same environment, though it does not of itself produce divergent forms of selection, opens the way for change in the habits of feeding with diversity of natural selection in the different sections of the species. Take, for example, the species of *Achatinella*: in Manoa and Mikiki they chiefly occupy the Kukui (*Aleurites triloba*) and other trees, while in Kawailoa and that region they neglect the larger trees and take to the Lobelia and other shrubs and herbaceous plants.

But why should the degree of divergence increase with the continuance of the Segregation? The answer seems to be that the combined effects of the different principles of transformation in the segregated groups increase with the time of segregation; and, as independent transformation is never parallel, the divergence increases in the same ratio. Diversity of natural selection is undoubtedly one of the principles producing this divergence, even when the vegetation and physical conditions of the different districts are the same, for when the habits of feeding change, the natural selection must usually change. But there are cases of divergence accompanying Segregation in which the habits of feeding seem to have remained unchanged; and in such cases I explain the divergence in part by the principle that separation always involves more or less segregation, and in part by the influence of the four principles which I have called Assimilational, Eliminational, Amalgamational, and Fecundal Transformation. Of these, Eliminational and Amalgamational Transformation are perhaps the most constantly operative. The principle of unbalanced Elimination is closely allied to the principle that separation involves Segregation; for both represent phases of the fact that any small fragment of a species is incapable of propagating all the qualities of the species in the exact proportion presented by the average of the species.

Similar Facts in other Fields.

Many of the facts embodied in these eight propositions must have been observed wherever naturalists have studied the geographical distribution of the varieties and species of polymorphic genera; but in the distribution of the *Achatinellinæ* there are features of peculiar interest arising from the fact that the powers of migration possessed by the species of the surrounding environment are very much greater than those possessed by the *Achatinellæ*. Through this circumstance a comparatively uniform environment is produced in which the effects of Independent Generation unmodified by the effects of changed environment may be observed. The remarkable facts of distribution which we have on the island of Oahu are found in other parts of the Sandwich Islands, wherever this family occurs. I am also fully convinced that, in other parts of the world, wherever one genus or family of very low powers of migration is surrounded by a body of plant and animal forms possessing much higher powers of migration, these similar facts will present themselves whenever investigation is made.

The distribution of land-mollusks belonging to the genus *Partula* found on the Society Islands presents similar features. The island of Reiatea, which is but 14 miles in length and 3 or 4 miles in breadth, is the home of about 30 species and varieties, most of which are confined to areas only a few square miles in extent. I am not informed as to the distribution of the vegetation on which these species feed, but there is no reason to suppose they occupy limited districts corresponding to those occupied by the different species of *Partula*.

Divergence in Insects.

The dependence of divergence on some form of Segregation is most clearly exemplified in insects, and though my studies are but limited in that field, I shall refer to a few cases, which may serve to direct attention to a class of facts of the highest interest not only to Entomology but to general Biology.

Divergence in the Species of the Lepidopterous Genera *Erynnis* (*Pamphila*) and *Thanaos* (*Nisoniades*).

These two genera of small North-American butterflies are worthy of the special attention of those who are studying the problems of divergent evolution; for they furnish strong indications that organisms which are with difficulty distinguished from each other by external form or colour, may, nevertheless, be well established species—segregated presumably by sexual instincts corresponding to sexual characters by which those of opposite sexes of the same species readily recognize each other, and probably cut off from the possibility of producing hybrids through incompatibility of physiological endowments. In the origin of some of these species Geographical Segregation may have had an important influence; but concerning others there can hardly be a doubt that the segregative influences, holding apart species that occupy the same districts, were, from the first, peculiarities of their sexual instincts and constitution. The reason for accepting this view of their origin is found in the fact that, though slightly divergent in other points, the characters by which they are clearly distinguished are found in the forms of the male genitalia; and in the characters of these organs we find clearly marked species, for the most part free from the intergrading forms which would certainly be presented if the different species were not prevented from crossing by sexual instincts or constitution.

A full description of these genera, with observations on the asymmetrical development of the right and left sides of the genital armature in *Thanaos*, will be found in Scudder's 'Butterflies of New England;' see also Mem. of the Boston Soc. Nat. Hist. ii. (1874), and Proceedings of the same Society for April 27, 1870, vol. xiii. p. 282 (1871).

Divergent Species of *Basilarchia*.

Basilarchia (Scudder) is an attractive genus of butterflies peculiar to North America, where it is represented by four or five species. Three of these are found in New England, and are minutely described in Scudder's 'Butterflies of New England,' from which I draw my information (pp. 250–305).

The distribution of these three species is of great interest, as it illustrates divergence both with and without Local Segregation. *B. Archippus* ranges over nearly the whole of the United States and over the southern portion of Canada. *B. Astyanax* occupies the valley of the Mississippi and eastward to the Atlantic from the Gulf of Mexico on the south to the lakes on the north. *B. Arthemis* is distributed from Newfoundland

and Nova Scotia on the east, over New England, Canada, the region of the lakes, away to the north-west, toward the confines of Alaska. It will be observed that the area of distribution of *B. Archippus* includes the whole of that of *B. Astyanax* and a large portion of that of *B. Arthemis*; while the areas of *B. Astyanax* and *B. Arthemis* overlap along the whole northern border of the territory occupied by *B. Astyanax*. This area of overlapping distribution in which the three species are associated is about a thousand miles in length, and from one hundred to one hundred and fifty miles in width.

Forms of Segregation that separate B. Archippus *from* B. Astyanax *and* B. Arthemis.

It is evident that, in the present condition of distribution, geographical barriers and territorial separation have nothing to do with the integrity of *B. Archippus* as a separate species. In other words, it is not under the influence of Geographical or Local Segregation. Whatever may have been its past history, these certainly are not the causes that at present prevent it from interfusing with other species of *Basilarchia* with which it is associated.

Again, Seasonal Segregation seems to have but little influence; for, though *B. Archippus* seems to appear 15 or 20 days earlier than the other species, the remainder of the breeding-season, which extends over many weeks, is coincident.

The habits and feeding instincts of this species must tend to separate it somewhat from *B. Arthemis*, for this latter species frequents forest-regions, especially when elevated and hilly, while *B. Archippus* is found in the open country in fields and meadows, especially in low levels. The eggs of *B. Arthemis* are chiefly deposited on the species of birch and willow that are found on the highlands; while the eggs of *B. Archippus* are chiefly deposited on the willows and poplars found on the lowlands, though on the White Mountains it occasionally extends its range to as high levels as *B. Arthemis*. There is therefore between these species a slight degree of Industrial Segregation; but this partial segregation does not prevent their being often found in the same fields, and unless held apart by sexual instincts and by partial infertility, hybrids, which are now very rare, would be very common.

We are therefore lead to believe that diversity of sexual instincts, accompanied by a considerable degree of cross-sterility, is the chief cause preserving the independent character of this species. Except for the sexual Segregation and Segregate Fecundity there is every reason to believe that this species could never have arisen, or, if it had arisen as a variety in some isolated locality, would have been submerged in the allied forms when its wider distribution was reached. This conclusion, which has been reached by observing the general relations of the species, is confirmed by a minute examination of the structure of the three species. We find that while the male genitalia of *B. Astyanax* and *B. Arthemis* differ but slightly, those of *B. Archippus* are considerably divergent. This is an index of the psychological and physiological relations of varieties and species of no small importance; for a comparison of many species shows that differences of this kind are usually accompanied by corresponding degrees of segregation in sexual instincts and of cross-sterility. In other words, we find that difference in the male genitalia, which is a form of segregate structure, is an index of Sexual Segregation and Segregate Fecundity.

The partial Segregation of B. Astyanax *and* B. Arthemis.

In the relations of these two species we find examples of segregative influences differing somewhat from those that have just been found in the case of *B. Archippus*. Regional Segregation, with exposure to different climates and adaptations to different food-plants, has undoubtedly had an important influence in the formation of these species; but, in the part of the country where they co-exist, their life-histories correspond completely, and cross-unions seem to be frequent. The hybrid form has been described as a separate species, and some entomologists have classed it as a dimorphic form of *B. Arthemis*, but Scudder gives several reasons for believing that it is the result of cross-unions between these two species. There are, however, several reasons for believing that partial Segregate Fecundity exists between the two species; for, in the strip of territory where the two are associated they do not completely coalesce, as would be the case if they were completely cross-fertile. In Scudder's 'Butterflies of New England,' pp. 159–160, we find mention of two species (*Cercyonis Alope* and *C. Nephele*), in which the cross-sterility must be considerably weaker than between the two species we are now considering; for, in the intermediate region in which their areas overlap, the intergrade forms are comparatively abundant. Moreover, the difference in the male genitalia of *B. Astyanax* and *B. Arthemis*, though much less than that which appears when either of these is compared with *B. Archippus*, is such as indicates a considerable degree of infertility.

In these two species we have then a good example of partial Segregation through distribution over areas, which, though overlapping, are for the most part distinct, reinforced by partial Segregate Fecundity which may or may not be accompanied by slightly divergent sexual instincts. There is also some Segregation resulting from the fact that the plants on which *B. Arthemis* seeks to deposit its eggs are chiefly the birches and willows of the hilly country, while *B. Astyanax* prefers fruit-trees of the Rosaceæ family, and other plants that are found in the more open country. These are, as I have shown in my paper on "Divergent Evolution through Cumulative Segregation," exactly the conditions that produce, in successive generations, increasing degrees of Segregate Fecundity.

Cumulative Segregation in the Formation of the above Species.

I judge that in the relations to each other of these three species we have the results of divergent evolution through cumulative segregation very clearly illustrated. In the earlier stages of divergence in this genus, *Basilarchia Archippus* with its fondness for the open fields must have become partially separated from the parent form from which both *B. Astyanax* and *B. Arthemis* have since sprung. The separation may have been in some measure due to what I have called Protectional Segregation; for we find that the form that has kept to the open country has through protective selection gained a very close resemblance to the colouring of *Anosia plexippus*, which is protected by its disagreeable qualities. The other form has probably gained compensative advantages by keeping closer to the woodlands. But the partial Segregation thus produced would never have resulted in constant specific differences if Segregate Fecundity had not arisen between the two forms. We may believe that some form of Impregnational Segregation (either Segregate Structure, Segregate Fecundity, or Segregate Vigour) was early introduced, and that under the protection of this barrier the specific distinctions of the two forms became fully established, though even now the barrier is not so complete as to entirely preclude hybrids between *B. Archippus* and each of the other species. Examples of both these hybrids are described by Scudder.

While this Segregation was being completed, one of the two forms thus created must have become subject to a new set of segregative influences, arising from wider distribution with diversity of climate and of habits of feeding, reinforced by a slight degree of Segregate Fecundity. *B. Astyanax* and *B. Arthemis* are the two species resulting from this last Segregation, and the process is so far from being complete, that wherever the areas of these two species overlap a hybrid form, which has been known as *B. Proserpina*, appears. That it is a hybrid is proved by the fact that it "varies most toward *Astyanax* where this prevails, and most towards *Arthemis* where that prevails," that it is found only in the narrow belt where the two species are brought into contact, and that it has been reported from so many points in this narrow belt that there is reason to believe that it occurs wherever the two species are brought into contact. If our exposition of the Segregations to which these species have been subjected is correct, they are cumulative in two respects—first because after one Segregation has been established another is superimposed, and second because a partial segregation established in one generation tends to become more complete in subsequent generations.

The primary causes in the whole process are the activities of the organisms acting upon each other and upon the environments in such a way as to produce, in the first place, Independent Generation with some degree of divergence, and then Unbalanced Natural Selection and other forms and transformation, which, acting upon selections of the species that are prevented from crossing, result in ever increasing divergence.

Divergent Evolution in the Periodical Cicada (*Cicada septemdecim*) *.

In this species we have examples of two quite distinct divergences, each depending on its own forms of Segregation, which are easily recognized.

The life-history of this insect covers 17 years and one or two

* My information is chiefly derived from the U.S. Department of Agriculture (Division of Entomology), Bulletin No. 8, by Dr. C. V. Riley.

months. The imago appears late in May, and for a little more than a month the males make the woods ring with their shrill stridulations. The eggs, which are deposited in the green twigs of trees, mature during the latter part of July; and each newly-hatched larva dropping to the ground, takes up a solitary subterranean life, which it follows till its period of 17 years is nearly complete. It then appears above the ground, passes into its winged stage, and enters on a few weeks of social life which closes its career. This species is widely distributed in that part of the United States that lies between the Atlantic shore and the Rocky Mountains. It does not, however, occur in Minnesota, Northern Michigan, or Northern New England. It is, however, represented by two races in every respect the same, except that one has a life-history of thirteen and the other of seventeen years. The 13-year race prevails in the Gulf States, while in New England and the Middle States the 17-year race is alone found. In Illinois, Missouri, Kansas, and in several of the Southern States the two races occur in the same localities; but it is evident that even in such localities it is only once in 221 years that there will be any opportunity for crossing between them, and we are informed by those who have made a special study of the subject that they do not cross when these opportunities occur.

These two races are therefore protected by partial Local Segregation; by Cyclical Segregation rendering it impossible that a brood of each occupying the same locality should have opportunity for crossing more than once in 17 generations of the shorter-lived race, or once in 13 generations of the longer-lived race; and by Sexual Segregation that shows itself in diversity of instincts preventing them from pairing when other conditions favour.

Whether devices have been tried to induce cross-unions, and whether such unions are unfruitful, I have never heard; but the simple fact that 15-year forms do not appear in localities where the two races are found, indicates that in nature they do not cross. Several such localities have been reported, but in none of them has an intermediate form been found. It seems, therefore, that we may safely draw the conclusion that we have here a case of complete Sexual Segregation between forms which to the human eye are undistinguishable, and which call their mates with stridulations which to the human ear are the same. Now I claim that in such races as these we have the beginning of divergent species—a beginning that lies in the segregative influences of constitutional and instinctive qualities persistently inherited by the two races, though the naturalist who examines specimens of the two races cannot distinguish them. All that is necessary to convert these two races into good species is the transformation of one or both of them while they are thus prevented from crossing; for we may be assured that the results of transformation under such circumstances will never be completely parallel.

Each of these races is again subdivided; for accompanying each is a diminutive form, differing somewhat in colour, not so early by eight or ten days in its first appearance, producing a quite distinct stridulation, and showing no disposition to associate with the larger form. This small form was described in 1851 by Dr. Fisher as a new species under the name *Cicada Cassinii.* Dr. Riley, however, hesitates to receive it as a separate species because the differences presented by the male genitalia are not constant. He says "there are sufficient differences to separate the two forms as distinct; but while the hooks of the large kind (*septemdecim*) are quite constant in their appearances, those of the smaller kind (*Cassinii*) are variable, and in some few specimens are indistinguishable from those of the large kind. This circumstance, coupled with the fact that the small kind regularly occurs with both the 17- and 13-year broods, would indicate it to be a dimorphic form of the larger, and only entitled to varietal rank"*.

I consider this case as of equal interest with the previous one; for it is an example of complete segregation between the forms of one species through diversity in their instincts. Whether these divergent instincts are sexual or social may be a matter of question; but in either case they are effectual in preventing crossing.

If future investigation shows that the small form is often produced directly from the eggs of the large form, it will have but little claim to be regarded as a separate race; but even then, if the small form breeds only with its own kind, as has been reported by several observers, and if the offspring persistently reproduce the characters of the parents, it will have to be considered something more than a dimorphic form of the large one. It would, in that case, be a dimorphic form that is assuming the

* United-States Department of Agriculture (Division of Entomology), Bulletin No. 8, p. 7.

character of a species. If the two forms were without segregative sexual and social instincts, then, with cross-fertility, the small form would be rapidly absorbed by the large form, which greatly preponderates in numbers ; and with cross-sterility the small form would rapidly become extinct ; for, through the comparative scarcity of their numbers, the representatives of the small form would have but little chance of mating with each other.

On the other hand, if the Sexual and Social Segregation is complete, it matters but little whether the forms are mutually sterile, for the separate races or species will be protected by the Positive Segregation produced by the divergent instincts, even if the Negative Segregation, depending on structural incompatibility and lack of physiological adaptation, is entirely wanting. It is only when associated with Positive Segregation that is partial in its results, that Negative forms of Segregation become important factors in the preservation of diverging forms.

In animals that pair, Segregation through sexual and social instincts plays a similar rôle in giving pre-emptive power to the males of a given species over the females of the same species, that is played by Potential and Prepotential Segregation in organisms whose fertilizing elements are distributed by wind or water. In the one case Instinctive, and in the other Potential Segregation, arising between varieties of the same species, marks these varieties as being the initial forms of divergent species.

This species presents another form of Segregation which is of much interest, though it has not yet resulted in forms that can be ranked as different races. I refer to the complete Cyclical Segregation that exists between the different broods of a given race appearing in different years. Of the 13-year race there are seven broods, and of the 17-year race fourteen. As an example of different broods occurring in the same region I would mention the two broods in the district of Columbia, one appearing in 1885 and at intervals of seventeen years thereafter, and another appearing in 1894 and at intervals of seventeen years thereafter. We have no means of testing the sexual or social instincts of these different broods, for they never appear in the same year. No one can say whether if they could be brought together they would be found as indisposed to breed with each other as are the 13-year and 17-year races. But, be that as it may, the two forms are as completely segregated as they can be, and the opportunity for independent, and therefore divergent, transformation is much the same as that which exists between the 13- and 17-year races. Two or three of the States have but one brood each; but in Ohio seven 17-year broods are reported, and in North Carolina one 13-year and six 17-year broods. I judge, however, from the reports that, even in these last-mentioned States, there are but few places, if any, where more than three broods overlap.

I have not seen any discussion of the causes that have produced these broods, but if we may believe that they have existed for a thousand generations, a possible if not probable cause is found in the unsettled conditions of climate that must have attended the breaking-up of the great ice-period. During years of diminished cold, colonies may have taken possession of regions which were too cold for their development at the return of the 17-year period when the offspring should have appeared; and still some of the benumbed and delayed pupæ may have survived, making their appearance one, two, three or more years later, when conditions were more favourable. The following observation referred to by Dr. Riley, in explanation of the accelerated or retarded appearance of sporadic individuals, throws some light on the origin of the different broods:—"That circumstances favourable or otherwise may accelerate or retard their development was accidentally proven in 1868 by Dr. E. S. Hull, of Alton, Ill., as by constructing underground flues for the purpose of forcing vegetables, he also caused the Cicadas to issue as early as the 20th of March, and at consecutive periods afterwards till May, though, strange to say, these premature individuals did not sing. They frequently appear in small numbers, and more rarely in large numbers, the year before or the year after their proper period. This is more especially the case with the 13-year broods"*. That climate has been an important factor in the development of the 13- and 17-year races is indicated by the fact that most of the districts occupied by the 17-year race lie north of lat. 38°, and most of those occupied by the 13-year race lie south of that line, though in Illinois there is a 13-year brood as far north as lat. 40°. Dr. Riley has not referred to the coincidence, but it seems to me a fact of some interest in this connection, that the southern limit of the great ice-cap which covered Canada and the northern part of the United States during the Glacial epoch extended along

* U.S. Department of Agriculture (Division of Entomology), Bulletin No. 8, p. 8, by C. V. Riley.

an irregular line between the parallels of lat. 38° and 40°. Lying south of the ice-region there was probably a considerable belt of country covered with pines and other conifers not adapted to the breeding of this species, so that both races, if they then existed, must have been crowded into the southern portion of the region now occupied by the 13-year race.

Instinctive and Cyclical forms of Segregation, such as cause the independent generation of the races and broods of this species, are usually associated with clearly developed specific distinctions relating to form, colour, and function. This does not, however, prove that the segregative divergence was subsequent to the general divergence in other respects; for if complete segregation continues for many generations it is likely to be followed by other divergences, and the divergent forms are then ranked as separate species. Moreover, the number of generations covered by the initial stage in which the different sections are only races is very small compared with those that are likely to be covered by the stages when they are separate species and genera. It is only, therefore, by rare chance that we find two forms that are still in the earliest stage of divergence and are, at the same time, completely segregated by constitutional differences. Again, segregative endowments are usually developed somewhat gradually; and while the segregation is advancing other transformations take place, so that by the time all crossing has come to an end the different sections have become well-marked species. Sometimes, as in the case of the three species of Butterflies already considered, there is more or less crossing after the sections have become quite distinct species. Such cases, however, as are presented by the 13- and 17-year races and by the different broods of this species of *Cicada*, show that complete segregation may be produced by the psychological and physiological constitution of different races, while distinctions of form, colour, and manner of call are entirely wanting so far as we can observe. This has seemed impossible to some naturalists, especially since Darwin has admitted that cross-sterility cannot be attributed to natural selection, and has therefore attributed it to the indirect effects of other qualities which have been produced by natural selection.

The great contrast in this respect between the species of *Basilarchia* and the 13- and 17-year races of *Cicada septemdecim* may perhaps be partially explained by the fact that the latter spend the greater part of their existence under ground, where the conditions have not been seriously changed since the close of the last glacial period. Again, one generation of the 17-year race of *Cicada* covers a period equal to that of thirty or forty generations of the *Basilarchia*, bringing thirty or forty fluctuations of climate, food, &c. to the latter, while the former is, for the most part, protected from serious fluctuations.

It is of course equally impossible to prove by all-inclusive observations, either that transformation is never completely parallel in sections of a species that are prevented from crossing, or that independent generation long continued is sure to result in independent transformation, and therefore in divergence ; but it is of no small interest that we find in the 13-year and 17-year races of this species the strongest proof that there are sometimes divergences which our senses do not perceive. If our senses were a sufficient test, it might be maintained that between these races a high degree of local and Cyclical Segregation has existed for many generations, without any other form of transformation having arisen to increase the divergence ; but if our informants are correct when they tell us that these races do not cross when appearing in the same district and at the same time, we need not hesitate to affirm that there must be some distinguishing characteristics by which those of one race are able to find each other, as well as segregative instincts which lead them to choose each other's society ; and, even if our informants are mistaken in supposing that cross-unions do not occur, there must be some form of incompatibility between the two races, resting on divergent endowments ; for otherwise we should find hybrid descendants with periods of more than 13 and less than 17 years' duration.

Concluding Remarks.

Outline of the Argument in support of the Theory of Divergent Evolution through Cumulative Segregation.

(1) The invariable experience of mankind in producing domestic races shows that Segregation is a controlling factor. The Segregation that produces domestic breeds and races is found to be of two kinds : first, that which is produced by men who designedly preserve the different styles of variation presented by one species, while at the same time they prevent them from crossing; and, second, that which commences in the indiscri-

minate division of the species into sections that are prevented from freely crossing through their being under the care of separate tribes of men, and which is changed into decided Segregation through the diversity of selection, or of some other transforming principle, to which the different sections are sure to be exposed; for it is found that these principles when brought to bear on separated sections never produce completely parallel effects.

(2) The paramount effects of Independent Generation having been shown in the broad fields of biological experiment presented by the domestication of plants and animals, the question is next raised whether species in a state of nature are subjected to influences dividing the individuals of one species into sections that are prevented from crossing; and if they are, how far this Independent Generation involves Segregate Generation.

In my paper entitled "Divergent Evolution through Cumulative Segregation" it was shown that there are many classes of activities by which the individuals of a species are thus divided, and that, in the majority of cases, the very process that separates them assorts them into classes with reference to one or more points of character; thus producing segregation that is completely parallel in its character to the segregation that is designedly produced by the pigeon-fancier between his various breeds of pigeons.

In the earlier half of the present paper I have shown that the indiscriminate division of the species, which often results from migration or geological changes, and sometimes from other causes, inevitably involves some Segregation; and whenever the transforming influences of the other factors of evolution begin to operate in the different sections, this initial Segregation is inevitably intensified and the divergence increased; for it is in the last degree improbable that change produced by these principles of transformation in sections that are prevented from crossing should be completely parallel in the different sections, even when exposed to the same environments. Having shown that the forms of Segregation produced in nature are analogous to those produced in artificial breeding,—

(3) The last step is to show, as has been attempted in the latter half of the present paper, that the relations to each other of varieties, species, genera, and the higher groups are such as would necessarily be presented if all such differences were the result of evolution that is always dependent on some form of

Segregation, but not always on diversity of natural selection, nor always on exposure to different environments.

We have found that persistent differences, whether varietal, specific, or generic, are not all adaptational, for some of them have no relation to utility ; and that adaptational differences are not all advantageous, for some of them relate to adaptations that would meet with equal success if the organisms should exchange habitats ; but that in every case divergence, whether utilitarian or non-utilitarian, whether advantageous or disadvantageous, is not maintained without Independent Generation.

Reply to Criticism.

In view of the examples of divergence that have been discussed in this paper, I think I may state, as in my previous paper, "It is therefore evident that the simple fact of divergence in any case is not sufficient ground for assuming that the divergent form has an advantage over the type from which it diverges" *. Mr. Wallace has criticised this statement, using the following words †:—"It seems to me that throughout his paper Mr. Gulick omits the consideration of the inevitable agency of natural selection, arising from the fact of only a very small proportion of the offspring produced each year possibly surviving. . . . . He omits from all consideration the fact that at each step of the divergence there was necessarily selection of the fit and less fit to survive ; and that if, as a fact, the two extremes have survived, and not the intermediate steps that led to one or both of them, it is a proof that *both* had an advantage over the original less specialized form." But what if the type from which the new form diverges is surviving at the same time that the new form survives ? And what if both the forms are surrounded by the same environment which they use in different ways ? Where then is the proof that the newer form has an advantage over the older form ? This was the class of facts I had been considering in the preceding paragraphs, which led to the conclusion criticised by Mr. Wallace ; and instead of omitting "the consideration of the inevitable agency of natural selection," it was the very thing I was considering, as will be seen by referring to p. 213. I had pointed out, that when a segregated portion of a species exposed to the

* Linnean Society's Journal, Zoology, vol. xx. p. 214.

† Nature, vol. xxxviii. p. 491.

same environment changes its habits, learning to appropriate resources that had not been previously used, it becomes a new intergenerating group "*in which a new and divergent form of natural selection is established*;" but that the result of the divergence thus produced is not necessarily advantageous, and may for many generations be somewhat disadvantageous. As I was aware that many naturalists would consider it absurd to suppose that disadvantageous, or even non-advantageous instincts, ever persist and become the occasion of divergent selection, I referred to Darwin's opinion that such might be the case with sexual instincts, and that the progenitors of man were deprived of their hairy coat by sexual selection that was, in its earlier stages, disadvantageous. I am not aware that Darwin has ever attempted to show how divergent sexual instincts arise and become permanently fixed as distinguishing characters of varieties and species. "The Advantage of Divergence," the principle on which he relied to account for divergent habits, producing divergent natural selection, he never attempted to apply here; and, above all, when he believed the newer instinct to be either non-advantageous or disadvantageous, as contrasted with the older instinct, he certainly could not have attributed advantage to the resulting divergence. As I have pointed out on previous occasions, Darwin assumed a psychological divergence in the sexual instincts of a species in order to account for the divergence in their secondary sexual characters relating to form, colour, &c.; and as there is no reason given why the psychological divergence should take place, or why it should precede the change in form and colour, the theory of Sexual Selection, as presented by Darwin, is incomplete and unsatisfactory, especially in its relations to divergent evolution. If he had thrown light on the causes of divergence in sexual instincts, he would have found the same or similar principles applicable to the explanation of divergence of all kinds. But my object in referring to his opinion here is to point out that he was free to admit that permanent divergence in sexual instincts may be non-advantageous, or even somewhat disadvantageous; and if this is true of sexual instincts, I do not see why it may not be equally true of industrial instincts. I think there is ample evidence that, when segregation has been established, divergence which is neither advantageous nor disadvantageous often arises in industrial as well as other instincts, and that these instincts may introduce new forms of natural, sexual, or social selection. The relations which exist between habits and their objects are in many species constantly varying in such a way as to constitute a series of experiments ; and when independent generation exists between different sections of a species, there is nothing to prevent divergence in the results of those experiments in the different sections, even when exposed to the same environment.

In Darwin's 'Posthumous Essay on Instinct,' published as an Appendix to Romanes's 'Mental Evolution in Animals,' on pages 378–384 mention is made of certain "imperfections and mistakes of instinct," and of certain instincts "that are carried to an injurious excess," and of others that are "small and trifling." Of the last-named he says :—"I have not rarely felt that small and trifling instincts were a greater difficulty in our theory than those which have so justly excited the wonder of mankind; for an instinct, if really of no considerable importance in the struggle for life, could not be modified or formed through natural selection." After mentioning several which might perhaps be considered trifling but are really of great importance to the species, he alludes to a few that seem to be "mere tricks" or "habits without use to the animals." Mr. Romanes, referring to these cases, offers the following explanation on p. 275 of the same work (I quote from the New York edition, Appleton & Co., 1884) :—"We have seen abundant evidence that non-adaptive habits occur in individuals, and may be inherited in the race. Therefore, if from play, affection, curiosity, or even mere caprice, the animal should perform any useless kind of action habitually. . . . , and if this habit were to become hereditary in the similarly constituted progeny, we should have a trivial or useless instinct." As an example of a strongly inherited non-adaptive instinct in a wild creature may be mentioned the cackling of the wild hen of India after having laid an egg. This habit is referred to by Darwin as one that may be slightly detrimental; but all that is necessary to put it beyond the developing influence of natural selection is that it should fail of bringing advantage to the species ; and that it is of no advantage will, I think, be generally admitted. If, then, species differ in regard to instincts that are non-advantageous, they are liable to present non-advantageous differences in form and colour, resulting either from the same causes that have produced the divergent instincts, or from divergent forms of natural, sexual, and social selection produced by these instincts; it will, however, be found that Segregation is the cause, or at least the necessary condition, on which the divergence depends.

In the present paper I have mentioned cases, representative of multitudes of others, in which there is divergence between two varieties or species occupying different districts, but surrounded by the same environments. In such cases, the differences presented by the separate forms and the divergence by which the differences have been produced, cannot be regarded as advantageous; for if the forms should exchange districts, the environment being the same, no disadvantage would be experienced; and this is equally true whether the differences relate to industrial adaptations, or to adaptations between the sexual instincts and the other secondary sexual characters of the group, or to characters that are absolutely non-utilitarian.

Mr. Wallace says that, in my previous paper, he looks in vain for any proof that cumulative segregation produces cumulative divergence; but at the same time, he claims that the segregation of which I speak, and which I have illustrated by a supposed case in the breeding of pigeons, is a form of selection which he calls "selection by separation." Adopting his phrase for the moment, I understand that he fully admits that in domestication "selection by separation" will produce divergence. Does he then doubt that the same process produced by natural causes will result in divergence? Or does he deny that "selection by separation" ever takes place in nature? He will probably grant that wherever natural causes act upon the representatives of a species in such a way that in each generation those presenting one style of variation are led to breed together and are prevented from breeding with other kinds, there divergence will certainly follow. This is what I call Segregation. That without it there is no cumulative divergence, and that with it there is always divergence, is amply proved by the universal experience of man in the domestication of plants and animals. All that is lacking is the consistent application of our knowledge to the theory of evolution.

Segregation is a process of much deeper significance than indiscriminate isolation, with which he seems to confound it; and one which in nature arises from a wide range of causes, some of which I have pointed out. But isolation without assortment of the forms according to any principle by which those of a kind are brought together, is often transformed into Segregation by the operation of the principles of transformation in the isolated sections of the species. This change is often brought about by the difference of the environments to which the organism is exposed in the isolated areas. This one form of Segregation has been clearly pointed out by Darwin, though he did not recognize segregation as a necessary condition for divergence. There are, however, many other ways in which nature produces a similar result. Some of these are operative when the organism is distributed in isolated districts but surrounded by the same environment, and some of them have to do with the development of non-adaptative divergences, which cannot come under the cumulative influence of natural selection.

It thus appears that Independent Generation co-operating with Natural Selection is one form of the wider principle of Segregation, which, in its many forms, is the ever present condition preceding cumulative divergence. Whatever divides the representatives of a species in such a way that those of a kind are made to intergenerate while prevented from intergenerating with other kinds is a cause of Segregation. This is my definition of Segregation; and my theory is that whatever causes Segregation causes divergence, and without Segregation there is no cumulative divergence. Now, in order to refute the theory it is necessary to show either that Segregation does not take place in nature, or that it is not accompanied by divergence, or that divergence takes place without Segregation. As Mr. Wallace has not attempted to prove any one of these counter propositions, I think his criticism is aside from the main issue. Even if my paper presents "a body of theoretical statements" with "no additional facts," this does not show that the theory is incorrect or the new use of the old facts unimportant in the explanation of divergent evolution. 'The Origin of Species' was filled with new theories applied to old facts. The importance of Cumulative Divergence through Cumulative Segregation, if a fact, is admitted. Is it a fact? is then the question that needs to be discussed; but, if Segregation is supposed to be no more than Isolation, the discussion will be of little avail.

In the Journal of the Royal Microscopical Society, 1889, part i. pages 33–4, will be found an appreciative, though a very brief review of my theory, closing with the suggestion that fuller elucidation is needed of the alleged tendency in nature to transform separation, when long continued, into increasing segregation and divergence. Want of space in my first essay made it necessary to postpone the full discussion of this part of the theory; but in the present paper I have sought to point out some of the more manifest principles on which this general law of *Intension* rests. There are undoubtedly other principles of transformation, which, when combined with separate breeding, inevitably produce divergent instead of parallel evolution; but the principles pointed out in this paper are sufficient to establish the general tendency, and to show that natural selection is by no means the only principle on which the law rests. If we could obtain sections of a species presenting exactly the same average character, and if we could prevent all the principles of transformation from coming in to aid in the process, separate breeding under such conditions would perhaps never produce divergence; but, as separation never produces exactly equivalent sections, it always tends to introduce transformation, through changed or unbalanced action in principles that would otherwise be unchanged and balanced in their action and therefore without transforming influence, and transformation in the separated sections inevitably becomes divergence. We thus gain an explanation of the fact that Isolation, even when accompanied by exposure to the same environments, usually introduces divergent forms of Selection, natural, sexual, social, or dominational, and often new effects from the action of other principles. Independent Generation precedes and determines the possibility of the divergence, and if it is segregative, it also determines in a measure the form of the divergence; but if it is simply separative, the form of the divergence depends on some other principle or principles.

APPENDIX.

Construction of the Permutational Triangle.

In the last chapter of my paper on "Divergent Evolution through Cumulative Segregation" (p. 250) I referred to the Permutational Triangle, which I had constructed to facilitate the solution of a problem there raised in regard to the degree of probability of extinction that would, under certain conditions, result from Segregate Fecundity. The first four lines of the table were obtained by direct observation on the permutations of letters arranged to represent the pairing of animals entirely

The Permutational Triangle.

Factorials.				Factors.	Occurrents. (0)	Concurrents. Of the first degree. (1)	Second degree. (2)	Third degree. (3)	Fourth degree. (4)	Fifth degree. (5)	Sixth degree. (6)	Seventh degree. (7)	Eighth degree. (8)	Ninth degree. (9)	Tenth degree. (10)
					1						*The*	*Ini*	*tial*	*Num*	*ber.*
$\lfloor 1=$	$1=$	no. of *occasions.*	in 1st line.	(1)	0	1					*The*	*firs*	*t li*	*ne.*	
$\lfloor 2=$	$2=$	,,	in 2nd	(2)	1	0	1				*The*	*seco*	*nd li*	*ne.*	
$\lfloor 3=$	$6=$	,,	,, 3rd	(3)	2	3	0	1			*The*	*thir*	*d li*	*ne.*	
$\lfloor 4=$	$24=$	,,	,, 4th	(4)	9	8	6	0	1						
$\lfloor 5=$	$120=$	,,	,, 5th	(5)	44	45	20	10	0	1					
$\lfloor 6=$	$720=$	,,	,, 6th	(6)	265	264	135	40	15	0	1				
$\lfloor 7=$	$5,040=$	,,	,, 7th	(7)	1,854	1,855	924	315	70	21	0	1			
$\lfloor 8=$	$40,320=$	,,	,, 8th	(8)	14,833	14,832	7,420	2,464	630	112	28	0	1		
$\lfloor 9=$	$362,880=$	,,	,, 9th	(9)	133,496	133,497	66,744	22,260	5,544	1,134	168	36	0	1	
$\lfloor 10=$	$3,628,800=$	,,	,, 10th	(10)	1,334,961	1,334,960	67,485	222,480	55,650	11,088	1,890	240	45	0	1

lacking in instincts or qualities that secure the pairing together of those of one kind.

For example, let A, B, C represent three females of three varieties of pigeons, and a, b, c three males of the same varieties, all occupying one aviary. Now supposing they are devoid of Segregating instincts, and that they all pair, what are the probabilities concerning the pairing of the males with their own kind? These will be clearly shown by arranging the letters representing one of the sexes in one fixed order, placing the letters representing the other sex underneath in every possible permutation of order. If we make six experiments the probability is that in 2 cases none, in 3 cases one, and in one case 3, will pair with their own kind. These numbers constitute the four terms of the third line. The first, second, and fourth lines were constructed in the same way, but for the construction of the tenth line in this way I estimated that several years of constant writing would be required. The remaining lines here given were therefore constructed according to the following rules, which were discovered by studying the first four lines. The discussion of different methods of constructing the Permutational Triangle, and the interesting properties of the same when constructed, must be deferred; but I may say here that I believe it will be found an important instrument for estimating a large class of probabilities.

A	B	C
a	*b*	*c*
a	c	b
c	a	b
b	a	*c*
b	c	a
c	*b*	a

One method of constructing any line of the Permutational Triangle from the preceding line.

(1) Of any given line, any desired number, except the first, may be obtained by multiplying the preceding number of the preceding line by the factor of the given line and dividing the result by the figure marking the degree of correspondence of the column of the desired number. (2) The first number of any line is one less or one more than the second number of the same line, according as the factor of the line is an odd or an even number.